

## Morphological differentiation among Subsaharan and North African populations of the *Lemniscomys barbarus* complex (Rodentia: Muridae)

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*Abstract.*—Morphometric evaluation discloses patterns of craniodental variation which demonstrate that populations currently assigned to *Lemniscomys barbarus* consist of two species: *L. barbarus* (Linnaeus 1766) and *L. zebra* (Heuglin 1864). One species-group epithet is herein allocated to the junior synonymy of *L. barbarus* (*ifniensis* Morales Agacino 1935), ten to *L. zebra* (*spekei* De Winton 1897, *dunni* Thomas 1903, *convictus* Osgood 1910, *albolineatus* Osgood 1910, *manteufeli* Matschie 1911, *oweni* Thomas 1911b, *nigeriae* Thomas 1912, *olga* Thomas & Hinton 1921, *nubalis* Thomas & Hinton 1923, and *orientalis* Hatt 1935), and a lectotype is designated for *Mus zebra* Heuglin (1864). No subspecies are recognized for either species, but the substantial heterogeneity documented within *L. zebra* advises continued study of those populations. The geographic occurrence of *L. barbarus* is restricted to scrub vegetation along a narrow coastal strip in Morocco, Algeria, and Tunisia; whereas, *L. zebra* is widely distributed over dry grassland and savanna biomes south of the Sahara Desert, from Senegal in West Africa to central Sudan in East Africa, and southwards to northcentral Tanzania. *Lemniscomys hoogstraali* Dieterlen (1991), known only by the holotype from eastcentral Sudan, is retained as a third member of the *barbarus* group. The species *L. barbarus* represents another example of small mammal endemic to the Barbarian province (Maghreb) of northwest Africa.

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African grass mice of the genus *Lemniscomys* have been conventionally arranged into three species groups or complexes—*barbarus*, *griselda*, and *striatus*—defined principally by the striping pattern of the dorsal pelage (Hollister 1919, Ellerman 1941, Van der Straeten & Verheyen 1980). While the *griselda* and *striatus* species groups have attracted much revisionary attention over the past 20 years (Van der Straeten 1975, 1976, 1980a, 1980b, 1981; Van der Straeten & Verheyen 1978, 1979, 1980), the *barbarus* complex, or striped grass mice, has yet to receive the same careful review, an oversight which this study begins to redress.

As with other taxa named in the late 1800s through the early 1900s, forms eventually associated under *Lemniscomys barbarus* had been first described as full species (for example, *zebra* Heuglin 1864; *spekei* De Winton 1897, and *dunni* Thomas 1903). In 1910, however, Osgood diagnosed two new races of striped grass mice from British East Africa (*albolineatus* and *convictus*) that he assigned to *Arvicanthis barbarus* and at the same time reassociated *zebra* Heuglin and *spekei* De Winton as subspecies of *A. barbarus*. Whether or not he was continuing the polytypic approach advanced in his 1909 revision of *Peromyscus*, Osgood's nomenclatural assessments



Fig. 1. Map of North and Central Africa depicting the type localities (stars) of the fourteen species-group taxa allocated to striped mice of the *Lemniscomys barbarus* species group. The date in parenthesis below each name indicates the year of the description.

established the precedent for treating striped grass mice south of the Sahara Desert as geographic representatives of Linnaeus' (1766) *Mus barbarus*, a form described from the Barbary Coast of northwest Africa. The new trinomials that appeared in the early 1900s—*b. manteufeli* Matschie (1911) and *b. nigeriae* Thomas (1912)—observed Osgood's delineation of specific boundaries, and Thomas' (1916) subsequent designation of a type species and emended diagnosis stabilized the contents and usage of *Lemniscomys* for African grass mice.

Still, an inclusive species definition was not universally or immediately adopted. By the time of Allen's (1939) systematic checklist of African mammals, three nom-

inal species of the *barbarus* complex were thought to inhabit Subsaharan savannas: *L. barbarus* proper (including *albolineatus*, *convictus*, *ifniensis*, *manteufeli*, *nigeriae*, *spekei*, and *zebra*), *L. dunni* (including *nubalis* Thomas & Hinton 1923, and *olga* Thomas & Hinton 1921), and *L. oweni* (including *orientalis* Hatt 1935). Ellerman (1941), as he did for so many sweeping formulations of species limits of African small mammals, adopted a broad definition of *L. barbarus* and so consolidated most of these regional epithets as geographic races (Fig. 1). As an exception, he retained, without explanation, *L. olga* as a species with a restricted distribution in Niger and left the final nomenclatural step to Rosevear, who in

1969 ranked *olga* as a subspecies of *L. barbarus*.

Ellerman's (1941) influential classification of *L. barbarus*, amplified by Rosevear's (1969) later reassignment of *olga*, is generally observed in recent African catalogues and mammalian checklists (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1991, Musser & Carleton 1993). The only other currently recognized species allocated to the *barbarus* group is *L. hoogstraali*, a member from southern Sudan recently described by Dieterlen (1991) and known only by the holotype (Fig. 1). Dieterlen, however, did not address the substantial variation apparent within *L. barbarus*, a widely distributed species with isolated populations in northwest Africa and with others occurring over savannas south of the Sahara Desert, from western (Senegal) to eastern Africa (Kenya and Tanzania). The appreciable variation across this region was remarked upon by Lamine Cheniti & Sami (1989), who noted that their Tunisian specimens of *L. barbarus* more closely resembled Central African *L. striatus* in size than West African *L. barbarus* (*b. nigeriae*, *b. olga*, and *b. oweni*). In this study, we examine the level of differentiation between the northwestern and Subsaharan moieties, the former the geographic source ("Barbaria") of *Mus barbarus* Linnaeus (1766), the type species of the genus, and the latter known by many regional epithets, the oldest of which is *Mus zebra* Heuglin (1864).

#### Materials and Methods

Approximately 650 specimens, representing about 170 principal collecting localities (Appendix 1), form the basis of this report. Specimens examined consist principally of skins with associated skulls contained in the museums, universities, or private collections listed below, each preceded by their institutional abbreviation. Except for *Mus barbarus* Linnaeus, which probably does not exist, type specimens of all species-group taxa we associate with the

*Lemniscomys barbarus* complex (Table 4) have been examined and measured by Van der Straeten.

AMNH	American Museum of Natural History, New York City
BEL	Bellier Collection, presently housed in the Universitair Centrum, Antwerpen
BMNH	The Natural History Museum, London
BZM	Museum für Naturkunde der Humboldt-Universität, Berlin
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	The Field Museum of Natural History, Chicago
HAP	D. C. D. Happold Collection of Mammals, Canberra
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel
KMMA	Koninklijk Museum voor Midden Afrika, Tervuren
MAKB	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
MCZ	Museum of Comparative Zoology, Harvard University
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Museum National d'Histoire Naturelle, Paris
NHRS	Naturhistoriska Riksmuseet, Stockholm
RUCA	Universitair Centrum, Antwerpen
SMF	Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt
SMNS	Staatliches Museum für Naturkunde, Stuttgart
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C.
ZMA	Zoologisch Museum, Amsterdam
ZMK	Zoologisk Museum, København

Fourteen cranial and two dental dimensions, distilled from a larger suite of variables previously defined by Van der Straeten & Van der Straeten-Harrie (1977), were recorded in millimeters (mm) to analyse

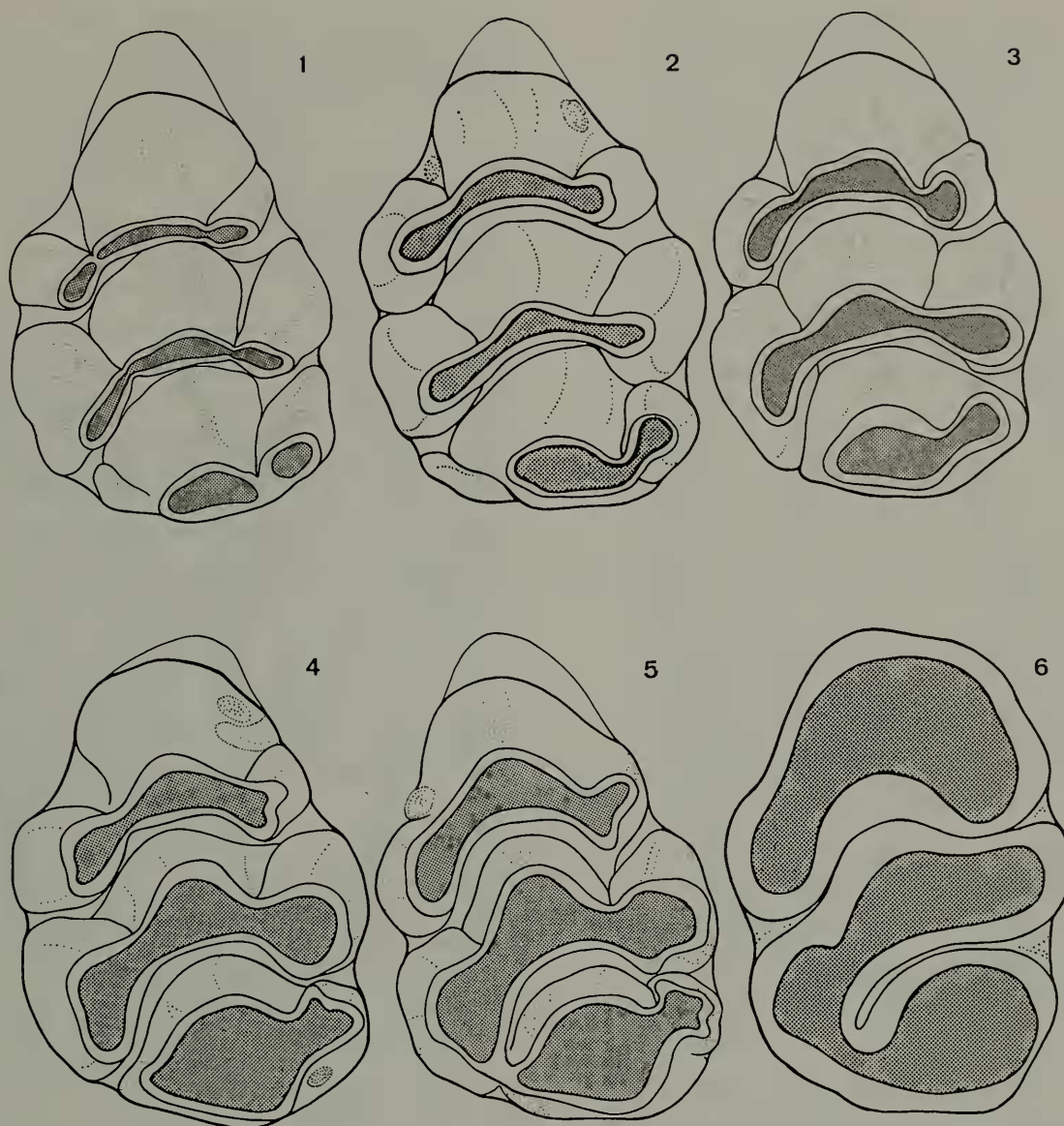


Fig. 2. Six age-classes based on toothwear stages, as defined by Van der Straeten (1980a:Fig. 1) for specimens of *Lemniscomys*.

univariate and multivariate variation within and between the populations sampled. To assess variation due to sexual dimorphism or post-weaning growth, gender was recorded from skin tags and specimens were assigned to one of six age classes. The age classes (Fig. 2) correspond to progressive wear patterns of the upper first molar as recognized by Van der Straeten (1980a).

Crania were viewed under a stereomicroscope when measuring the craniodental variables to 0.01 mm using hand-held digital calipers accurate to 0.03 mm. These 16 measurements, and their abbreviations as used herein, include (see Fig. 3 for landmarks): occipitonasal length (ONL); great-

est zygomatic breadth (ZB); breadth of the braincase (BBC); breadth across the occipital condyles (BOC); least interorbital breadth (IOB); length of nasals (LN); breadth of the rostrum (BR); postpalatal length (PPL); length of the bony palate (LBP); length of the upper diastema (LD); length of the incisive foramen (LIF); breadth across the upper first molars (BM1s); breadth of the zygomatic plate (BZP); length of the auditory bulla (LAB); alveolar length of the maxillary toothrow (ALM); and coronal width of the first upper molar (WM1). In addition, standard external dimensions and weight (in grams) were transcribed from skin tags as given by the

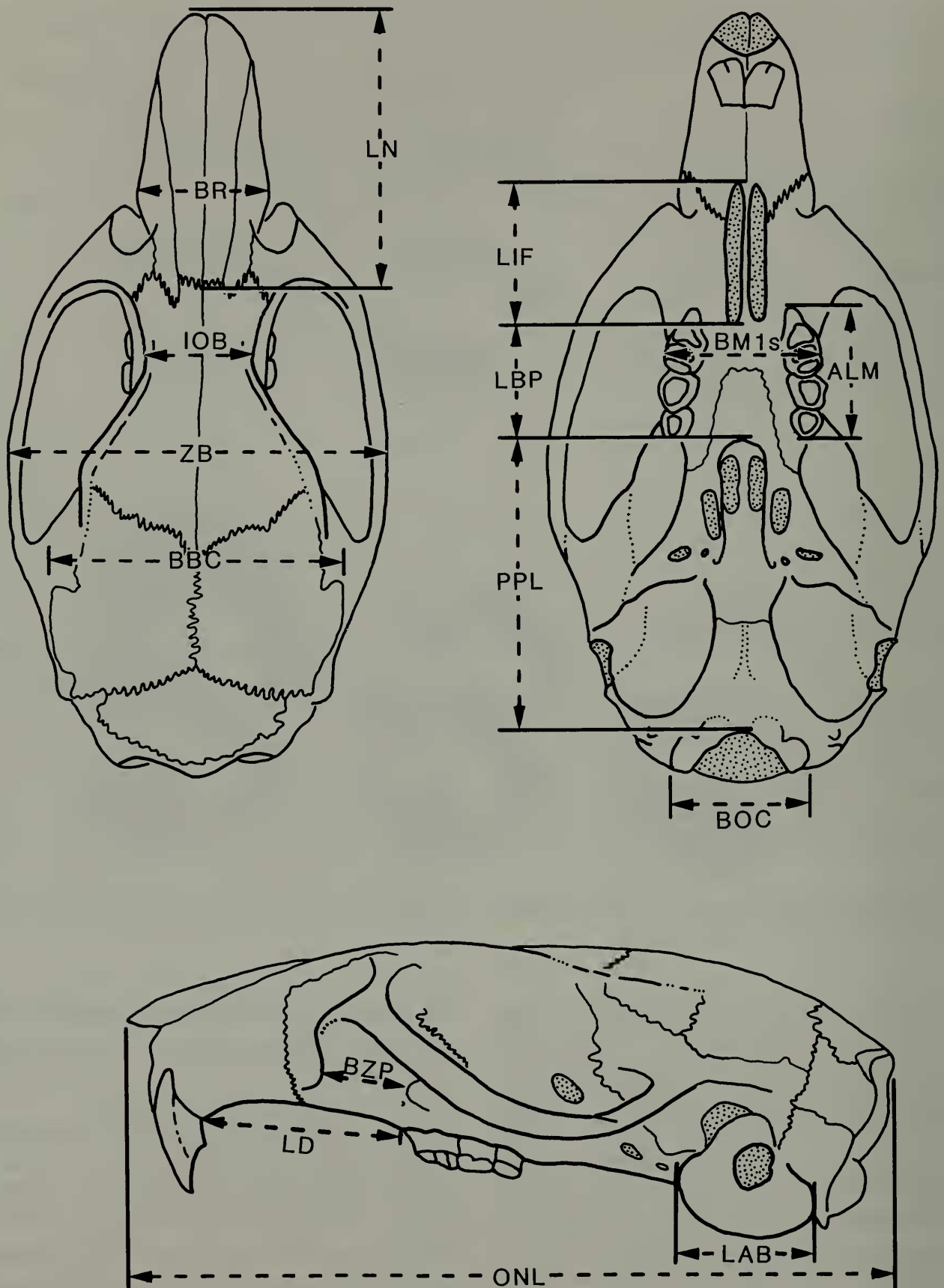


Fig. 3. Landmark points for 15 cranial measurements recorded in this study, as portrayed on dorsal, ventral, and lateral views of a schematic *Lemniscomys* skull (adapted from Van der Straeten & Van der Straeten-Harrie 1977:Fig. 1).

collector: total length (TOTL), tail length (TL), hindfoot length (HFL), and ear length (EL); subtraction of TL from TOTL yielded head-and-body length (HBL).

Several authors have commented on the relative scarcity of individuals of *Lemniscomys barbarus* in the field and the difficulty of obtaining them in adequate series (for example, Saint Girons & Petter 1965, Rosevear 1969, Happold 1987). We formed a similar impression based on the character of the museum samples we encountered, in which striped grass mice are usually represented by only one to a few specimens from a collecting locality. For certain multivariate analyses, specimens from localities over a general region were necessarily grouped as eleven operational taxonomic units (OTUs). These OTUs, arranged from northwestern toward eastern Africa, and their sample sizes are:

- OTU (1).— $n = 44$ , from Morocco, Agadir Province (USNM 475125–475148, 475150–475169);
- OTU (2).— $n = 15$ , from Morocco, Khouribga and Rabat provinces (USNM 475121, 475122, 475170–475182);
- OTU (3).— $n = 9$ , from Senegal, all localities (USNM 376529–376536, 380463);
- OTU (4).— $n = 24$ , from Ivory Coast and western Burkina Faso (FMNH 105180; USNM 465398–465400, 465413, 466674–466676, 466678–466693);
- OTU (5).— $n = 32$ , from Ghana and Togo, all localities (USNM 412746, 412747, 420570–420585, 435400–435405, 438311–438314, 466694–466697);
- OTU (6).— $n = 49$ , from eastern Burkina Faso, Benin, and westernmost Nigeria (USNM 397647, 404085–404087, 422058–422064, 422066–422083, 439580–439586, 450852–450855, 465401, 465404–465412);
- OTU (7).— $n = 51$ , from Nigeria, Jos Plateau, Panyam and vicinity (USNM 404020, 404022–404028, 404030–404039, 404044, 404046–404048, 404050, 404052–404056, 404058–404064, 404065–404069, 404071–404073, 404075–404078, 404080–404084);
- OTU (8).— $n = 11$ , from Zaire, Faradje and Niangara (AMNH 49610–49612, 49614, 49615, 49623, 49624, 49627, 49630, 49632, 49633);
- OTU (9).— $n = 13$ , from Uganda, Rhino Camp (AMNH 180121; CM 2850; USNM 165191, 165193, 165194, 165198, 165200–165205, 165422);
- OTU (10).— $n = 23$ , from Sudan, Equatorial Province, various localities (FMNH 35313, 35314, 66853, 66854, 66857, 66859, 66860, 67171, 67172, 67175, 67293, 79500–79502; USNM 165192, 299764–299766, 299768–299771, 318003);
- OTU (11).— $n = 15$ , from southcentral Kenya, various localities (AMNH 114446–114448, 187678, 187679; CM 57977, 98258, 102462, 102463; USNM 162884, 181737–181740, 437394).

Standard descriptive statistics (mean, range, standard deviation, coefficient of variation) were derived for the OTUs. One- and two-way analyses of variance, discriminant functions, and principal component analyses were computed using the 16 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and loadings are expressed as Pearson product-moment correlation coefficients of the components with the original cranial variables. Means and ranges of external variables are provided as a guidance in identification (see Appendix 2) but were not considered in multivariate analyses. Except for the a posteriori input of type specimens (all measured by Van der Straeten) to a discriminant function analysis (OTU series measured by Carleton), numerical results presented in the various ta-

bles and figures are not based on intermixture of craniodental data collected individually by the authors. All analytic procedures were conducted using Systat (Version 6.0, 1996), a series of statistical routines programmed for microcomputers.

### Results

*Morphometric analyses.*—Patterns of variation contingent upon age and gender cohorts within local samples of *Lemniscomys* generally conform to those presented for other species of African muroids (Van der Straeten & Verheyen 1978, Carleton & Robbins 1985, Carleton & Martinez 1991). That is, significant age-related size variation is apparent for certain variables, notably those measured at the cranial extremes (ONL, ZB) or on the rostrum (LN, BR, LIF, LD); whereas,  $f$  values of age effects derived from ANOVAs are smaller and typically insignificant for dimensions taken across the braincase (BBC, IOB, BOC) and on the molars (ALM, WM1). Sexual dimorphism in size or age-sex interactions contribute little to mensural variation within OTUs (Table 1). Critical estimation of such influences upon sample variation is sensitive to sample size and particularly to the balance of age and sex representation among the specimens available for measurement (Voss & Marcus 1992). Our inability to achieve these sampling ideals with the real museum series at hand presumably accounts for certain inconsistencies and differences in probability levels attained for our two largest OTUs (Table 1). Notably, the lack of significant mean size differences among age cohorts for external skin variables (TOTL, TAIL, HFL) and the occurrence of same for the alveolar molar length of the Moroccan sample (OTU 1) seem counterintuitive and at odds with previous studies.

For the two largest, geographically homogeneous samples—Morocco (OTU 1) and Nigeria (OTU 7)—nearly all cranial variables (except WM1) contribute substantial-

Table 1.— $f$ -values from two-way ANOVAs (sex and age cohort) for 3 external and 16 cranial dimensions in two large OTUs of the *Lemniscomys barbarus* group.

	OTU 1 (25 M, 19 F)			OTU 6 (26 M, 23 F)		
	Age	Sex	Inter-action	Age	Sex	Inter-action
TOTL	2.6	0.0	0.6	0.1	0.0	1.1
TAIL	2.3	0.1	0.2	1.1	0.8	1.3
HFL	0.6	1.3	0.2	0.1	0.1	0.4
ONL	5.2**	0.1	1.2	9.4***	0.1	1.7
ZB	8.2***	0.5	1.1	2.4	0.4	2.1
BBC	4.6*	5.7*	0.0	1.5	3.2	0.2
IOB	1.2	0.1	0.7	1.1	0.5	0.1
LN	1.2	0.1	0.8	6.4**	0.6	4.1*
BR	8.2***	1.5	0.7	4.5*	0.2	0.3
PPL	1.9	0.5	0.3	9.4***	1.3	2.1
LBP	4.5*	0.1	1.2	0.2	0.2	0.9
LIF	0.9	0.4	1.8	3.8*	0.2	0.3
LD	4.3*	0.1	1.9	10.2***	0.0	1.3
BM1s	5.0*	0.2	3.1	8.9***	4.1*	0.2
BZP	2.2	0.1	0.4	9.3***	0.0	1.0
LAB	1.2	0.6	0.2	2.2	0.2	1.4
BOC	0.5	0.3	1.3	1.5	0.2	1.0
ALM	0.7	0.7	0.8	8.7***	1.0	0.4
WM1	1.5	1.2	1.1	0.7	1.1	0.1

\* =  $P \leq 0.05$ ; \*\* =  $P \leq 0.01$ ; \*\*\* =  $P \leq 0.001$ .

ly and positively to variation (74.1%) summarized by the first principal component (Table 2). Their covariation accounts for the uniformly higher scores and right-oriented dispersion of the Moroccan specimens relative to those from Nigeria (Fig. 4A). Pearson correlation coefficients of the original variables and the second principal component are consistently smaller and occasionally negative; no biologically meaningful segregation of specimen scores is apparent among the minor variation (6.0%) represented by this axis. Age-related size increase may account for some dispersion along the first component within each geographic sample (Fig. 4B); however, for the comparison of these two samples, age-class influence is statistically negligible ( $f = 1.99$ ,  $P = 0.09$ ) relative to the pronounced locality effect ( $f = 121.1$ ,  $P \leq 0.001$ ) upon PC I scores.

Little overlap of individual scores between the Moroccan and Subsaharan sam-

Table 2.—Results of principal component analysis performed on OTU 1 (Morocco,  $n = 43$ ) and OTU 7 (Nigeria,  $n = 51$ ), the two largest samples available for the *Lemniscomys barbarus* complex (see Fig. 4).

Variable	PC I	PC II
ONL	0.99	-0.02
ZB	0.94	0.09
BBC	0.81	0.05
IOB	0.75	0.29
LR	0.91	-0.13
BR	0.83	0.10
PPL	0.94	-0.08
LBP	0.80	0.47
LD	0.97	-0.11
LIF	0.86	-0.47
BM1s	0.85	0.06
BZP	0.87	0.17
LAB	0.74	0.15
BOC	0.74	-0.02
ALM	0.67	0.05
WM1	0.19	0.02
Eigenvalue	0.049	0.004
% Variance	74.1	6.0

ples is observed in plots of the first two canonical variates derived from discriminant function analysis of the 11 defined OTUs (Fig. 5A, B). Again, the uniformly larger skull dimensions of the Moroccan series are emphasized by the high, positive loadings of nearly all cranial variables on the first canonical variate (Table 3); the width of the first molar as in the principal component analysis, is least influential in affecting the segregation of group means along the first canonical axis. Unlike the clearcut separation of the two Moroccan samples, those drawn from West (OTUs 3–7) and East (OTUs 8–11) Africa display appreciable intermixture of individual specimen scores projected upon the first two canonical variates (Fig. 5A).

Cluster diagrams generated either from Mahalanobis distances among group centroids (Fig. 6A) or from log-transformed OTU means (Fig. 6B) similarly underscore the strong phenetic separation of the Moroccan samples from those found south of the Sahara Desert. Among the latter, the clustering patterns suggest some association

according to geographic propinquity, but certain OTUs (Senegal and Kenya) discordantly merge with far distant samples.

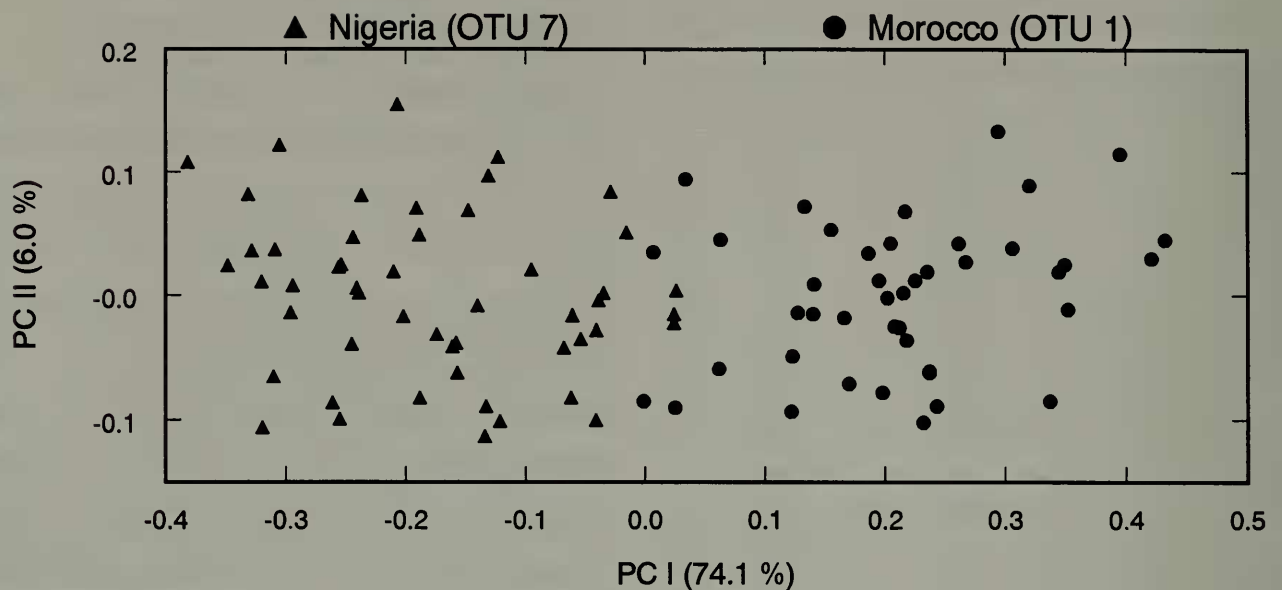
Posthoc numerical classification of ten type specimens with suitably intact crania was effected using the discriminant function statistics computed from analysis of the 11 OTUs. Of the nine types representing taxa described from Subsaharan Africa, none was “correctly” classified with the OTU closest to their geographic origin; for example, *albolineatus* and *convictus*, both named from Kenya, were predicted to have membership in Ivory Coast-West Burkina Faso (OTU 4) and East Burkina Faso-Benin (OTU 6), respectively, and *manteufeli*, named from Tanzania, was allocated to Sudan (OTU 10). Nevertheless, all type specimens were sensibly associated within the range of multivariate dispersion exhibited by specimens from the general region of their collection: namely, Morocco (*ifnien-sis*) or the Subsahara (the remaining nine) (Fig. 7).

In summary, ordination analyses, whether extracting principal components from original measurement data or canonical variates from the centroids of 11 predefined geographic samples, reveal the more robust crania typical of the Moroccan samples as compared to striped grass mice from East and West Africa (Fig. 8). In contrast to our experience with other morphologically similar, congeneric species, features of shape or proportion are not evidenced by the dispersion of scores along the secondary axis of ordination; that is, the cranium of Moroccan *barbarus* seems to be an isometrically oversized version of that characterizing populations broadly distributed across Subsaharan savannas. Although not used in multivariate computations, parameters of bodily dimension and mass also convey the exceptional size of the Moroccan populations (Fig. 9, Appendix 2).

*Pelage comparisons.*—The upperparts of members of the *L. barbarus* complex are marked by longitudinally continuous, alternating dark and light stripes, a distinctive



A



B

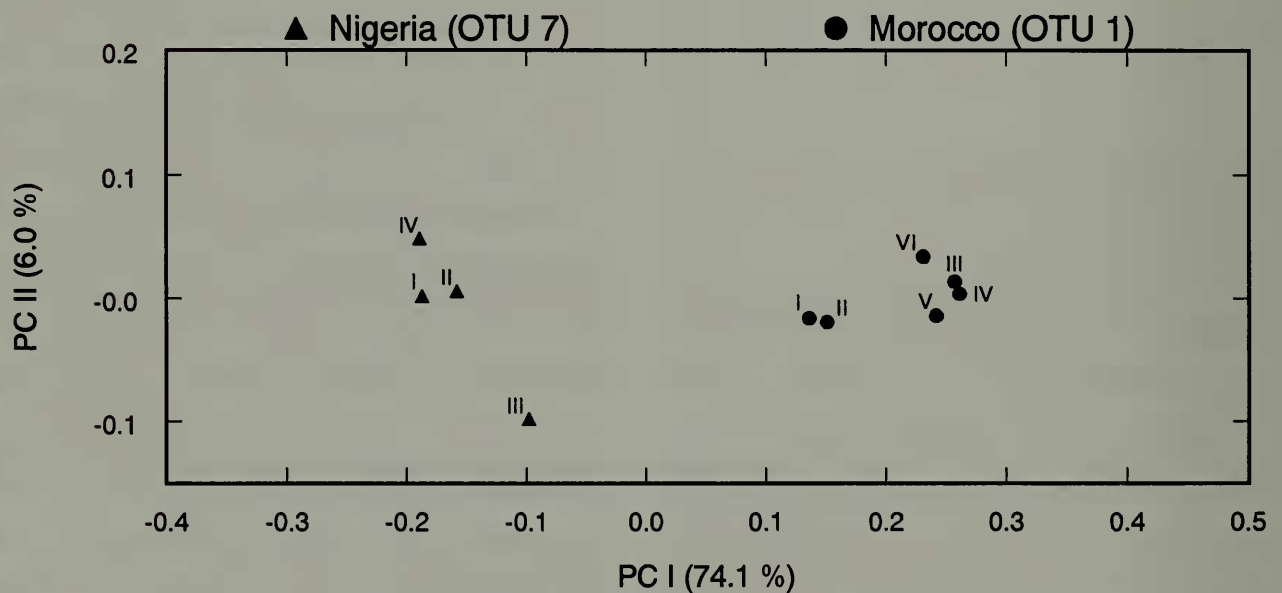


Fig. 4. Results of principal component analysis performed on 16 log-transformed craniodental variables measured on 94 specimens representing Moroccan (OTU 1,  $n = 43$ ) and Nigerian (OTU 7,  $n = 51$ ) samples of the *Lemniscomys barbarus* complex: A, projection of individual specimen scores on the first two principal components extracted (see Table 2); B, projection of centroids, as calculated a posteriori, representing six age classes within each OTU on same principal components (age classes V and VI not represented in the Nigerian sample).

pattern which readily contrasts to the single mid-dorsal line of the *L. griselda* group (single-striped grass mice) or to the variably interrupted or punctulated lines of the *L. striatus* group (spotted grass mice). Attention is here given to qualitative description of chromatic and pattern variation of the upperparts because such traits have histor-

ically received prominence in the diagnoses of taxa, whether named as species or subspecies.

General characterization of the pelage in the *L. barbarus* group follows (Fig. 9). The single vertebral line, which extends from the middle crown to the rump, typically possesses a deeper hue than that of the lat-

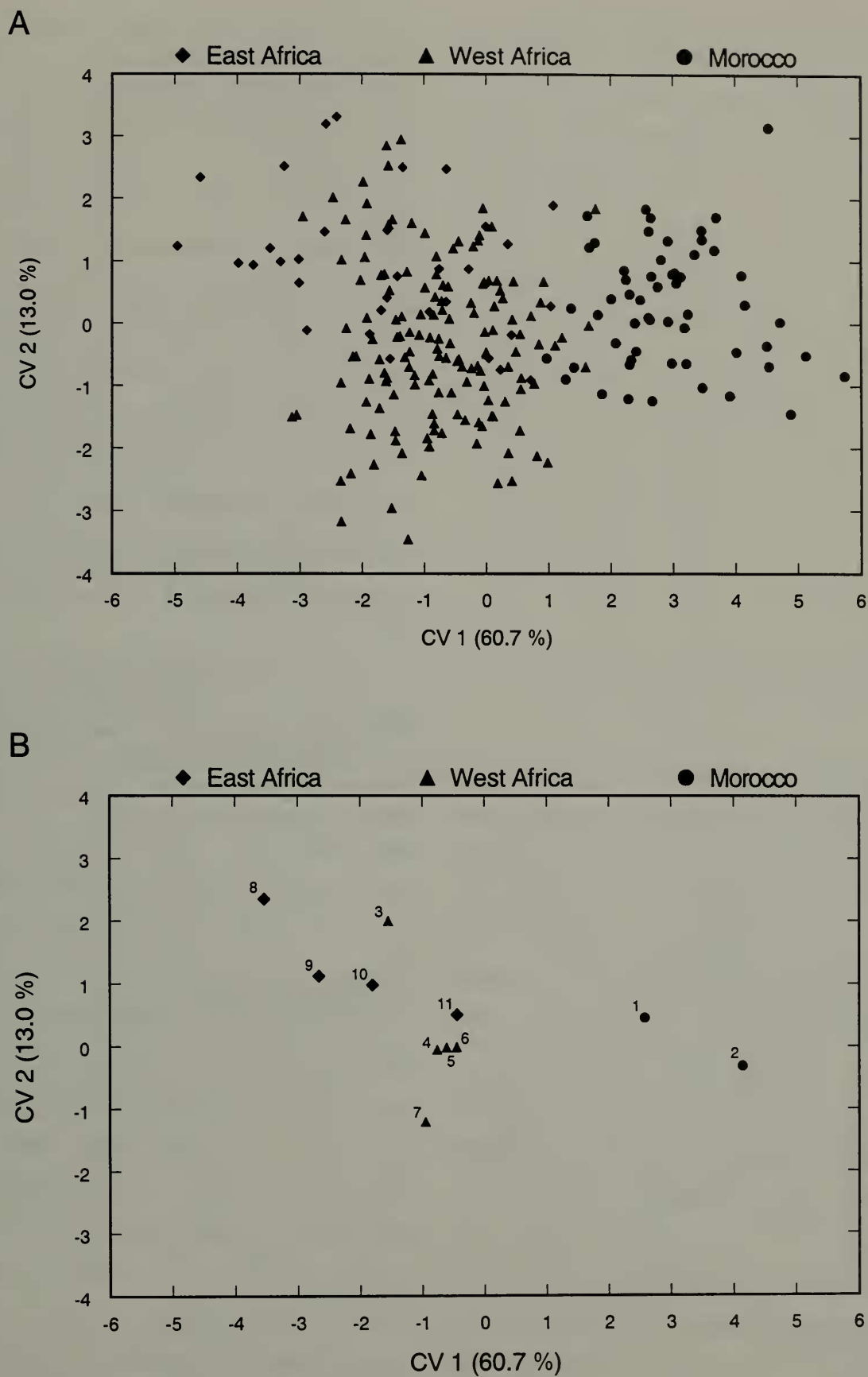


Fig. 5. Results of discriminant function analysis performed on 16 log-transformed craniodental variables measured on 235 intact specimens representing 11 OTUs of the *Lemniscomys barbarus* complex (see Table 3): A, Projection of individual specimen scores on first two canonical variates extracted; B, Projection of group centroids on first two canonical variates extracted.

Table 3.—Results of discriminant function analysis performed on intact specimens ( $n = 235$ ) representing 11 OTUs of *Lemniscomys* (see Fig. 5).

Variable	CV I	CV II	$f(\text{OTU})$
ONL	0.94	0.14	49.0***
ZB	0.94	-0.08	53.2***
BBC	0.75	-0.04	21.3***
IOB	0.70	0.04	19.2***
LR	0.87	-0.03	33.2***
BR	0.76	-0.06	21.5***
PPL	0.84	0.28	33.6***
LBP	0.75	0.16	18.0***
LD	0.91	0.23	43.7***
LIF	0.79	0.19	29.9***
BM1s	0.82	-0.21	29.9***
BZP	0.70	0.14	14.9***
LAB	0.70	-0.13	16.3***
BOC	0.65	0.23	13.4***
ALM	0.70	-0.09	15.4***
WM1	0.45	-0.49	9.3***
Canonical correlation	0.87	0.64	
Eigenvalue	3.25	0.69	
% Variance	60.7	13.0	

\* =  $P \leq 0.05$ ; \*\*\* =  $P \leq 0.001$ .

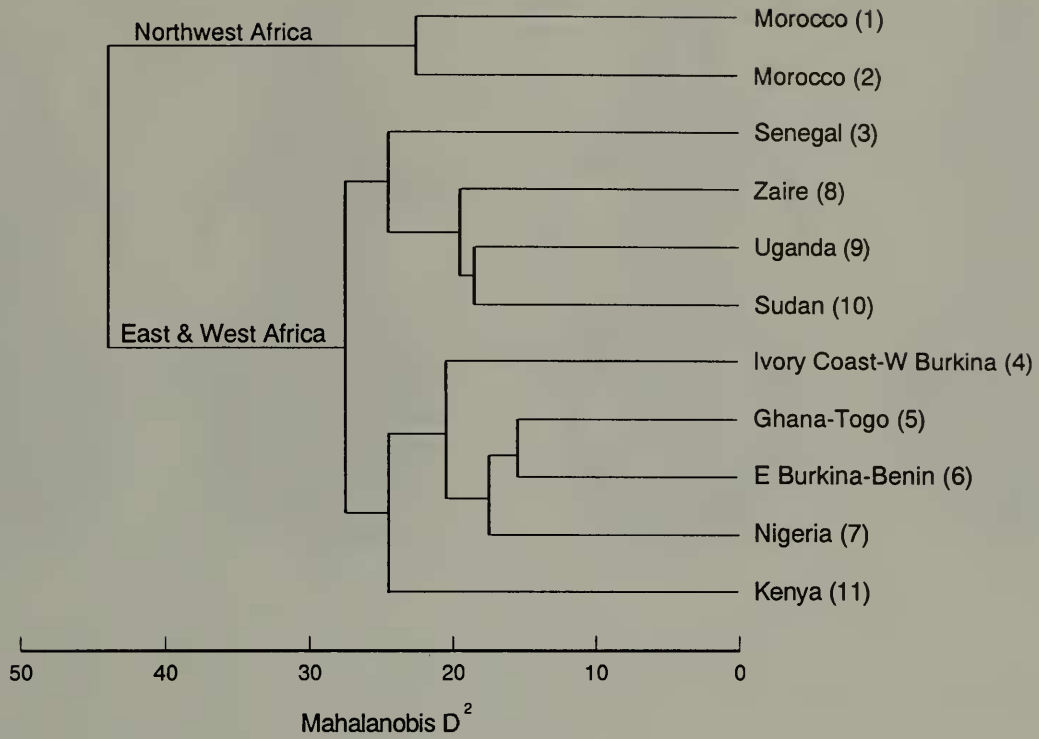
eral dark stripes, appearing black as compared to dark gray or brown. To either side of the mid-dorsal line occur four to six primary pairs of alternating light and dark stripes (as observed over the lumbar-rump region), whose definition more or less abruptly degrades toward the sides; the dark lines are usually wider than the intervening light ones. The venter is much lighter and unmarked, ranging from dull to bright white, and a clear buff lateral line may demarcate the dorsal-ventral pelage transition. Fine tawny to rufescent hairs densely clothe the pinnae and accent their contrast to the crown and dorsal pelage. Tops of the fore and hindfeet are covered with white to pale buff hairs. The tail is indistinctly bicolored, the dorsal hairs black and those underneath ochraceous to rufous, resembling the color of the pinnae.

Within and among locality samples of the *L. barbarus* group, one can discern several thematic variations around the chromatic groundplan described above. The distinctiveness of the mid-dorsal line varies with

respect to the dark lateral stripes, a consequence of its color (brown to dusky to black) and width. Thus, the mid-dorsal stripe may appear densely black and relatively wide (Figs. 9A, C) or brown and notably thin (Fig. 9B). The boldness of the striping pattern is modulated by the color of the dark bands (medium brown to black) in relation to the purity of the pale bands (clear white to warm buff or dull ochraceous) and by the degree of ochraceous suffusion over the middle dorsum. These chromatic subtleties interact to heighten or lessen the sharpness of the linear contrast (compare Figs. 9A to 9C, & D). The fine aural hairs range from nearly cinnamon, setting the pinnae conspicuously apart from the general dorsum (Fig. 9D), to dull ochraceous, lessening the visual distinction of the pinnae (Fig. 9A).

An important pelage variation involves the number of dorsal stripes, counts of which were mentioned regularly by the early describers. For example, Thomas (1903: 297) noted that *dunni* possesses "on each side, five uninterrupted buffy stripes, separated from each other by broad brown bands, each of which is divided down the centre into two by an uninterrupted band of light." Osgood (1910:11) characterized *convictus* as having: "Light stripes pale ochraceous buff and numbering 5-6 of the heavier or primary ones and 4-5 of the secondary ones on each side;" and "Four definite primary dark stripes on each side, each divided by a secondary light stripe." And Hatt (1935:2) cited the "six pairs of lateral dark stripes . . . distinctly split by secondary light stripes" in describing *orientalis*. The number of stripes is an inexact impression largely mediated by the development of these secondary light lines within the first, and sometimes the second, pair of primary dark lateral stripes (as numbered away from the unpaired vertebral stripe). Individuals with strongly penetrant secondary light stripes appear to be finely streaked with more and narrower light and dark stripes, especially over the middle dorsum (Figs.

A



B

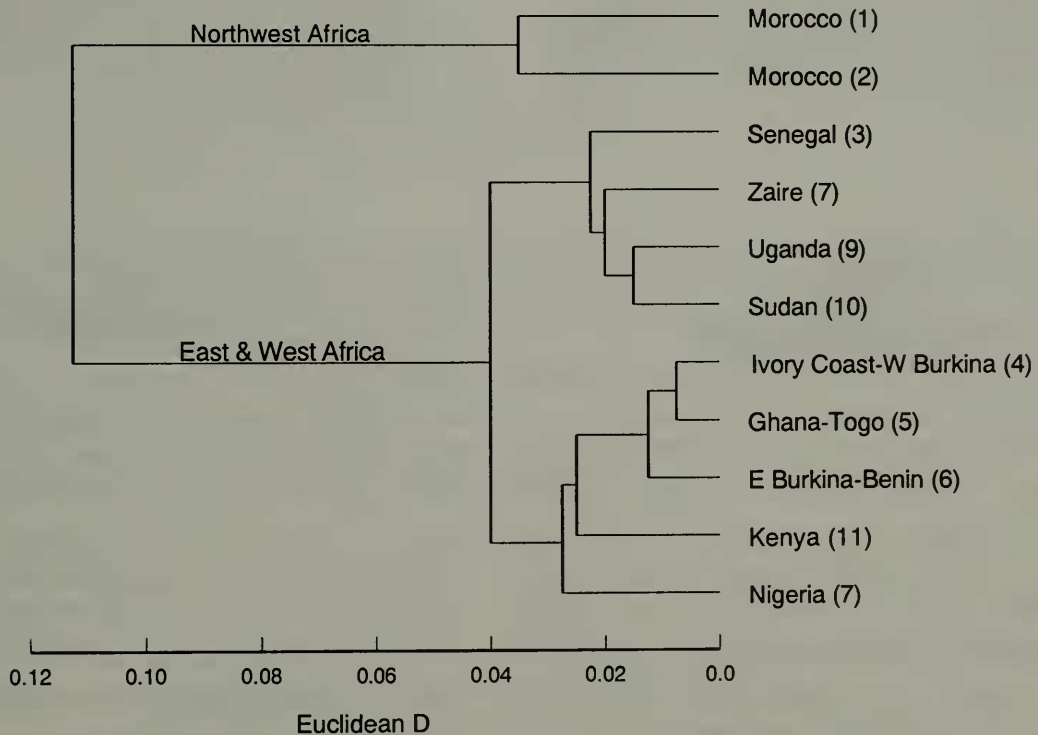


Fig. 6. Clustering (UPGMA) of 11 geographic samples representing the *Lemniscomys barbarus* complex, as derived from: A, Mahalanobis' distances ( $D^2$ ) among the OTU centroids (see Fig. 4); B, Euclidean distances between OTUs based on means of the 16 log-transformed craniodental variables.

9B, D); whereas, those that have obscurely defined secondary lines seem to have fewer and broader dark stripes on their upperparts (Figs. 9A, C—the latter specimen was pur-

posefully selected for its extreme expression of this consolidated pattern.).

The pelage characteristics reviewed above undoubtedly seemed easily definable

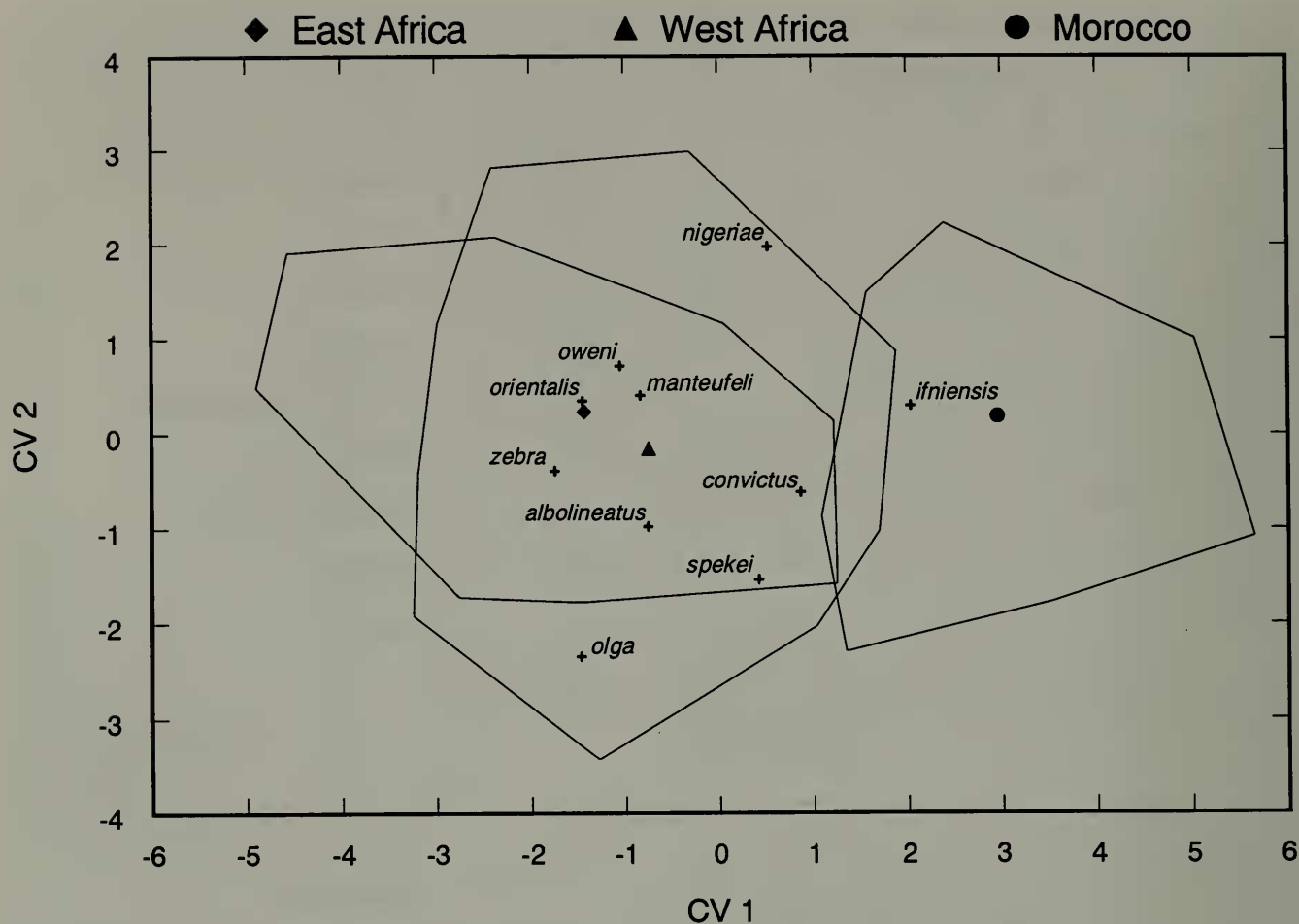


Fig. 7. Results of discriminant function analysis presented in Fig. 5, with a posteriori classification of type specimens representing ten species-group taxa of the *Lemniscomys barbarus* complex. Polygons enclose maximal dispersion of individual scores around group centroids for each geographic region.

and unique as exemplified by the holotypes and small hypodigms for the various epithets created in the late 1800s and early 1900s. However, as more specimens, larger locality series, and broader geographic representation have become available, the individuality of these color morphs is observed to break down and merge imperceptibly. By 1969, Rosevear concluded that even subspecific separation of West African *nigeriae* from *oweni*, originally assigned to separate species on the basis of having white versus buffy light stripes as purported by Thomas (1911b, 1912), was indefensible. We agree with Rosevear's assessment and further note that the occurrence of boldly marked striping versus more muted dorsal patterns—such as advanced to discriminate *albolineatus* versus *convictus* (Osgood 1910) or *nubalis* versus *dunni* (Thomas 1903, Thomas & Hinton 1923)—can be du-

plicated by extreme individual patterns just within USNM Nigerian series. Hatt (1935) identified the absence of facial stripes as a useful feature for sorting specimens of *nubalis* from those of *orientalis* and *zebra*. Nevertheless, we have found the continuation of trunk markings (the fourth lateral pair of light and dark stripes) onto the cheeks as highly variable within Sub-Saharan locality samples and doubt the trait's utility as a diagnostic tool at the level intended by Hatt (and see Discussion below). The hispid or spiny quality of the dorsal fur has been also mentioned in some descriptions of striped mice, but such textural differences are difficult to objectively convey and practically apply. And so forth for many of the pelage traits given as diagnostic criteria.

Certain geographic trends in pelage color and pattern do emerge with the better series

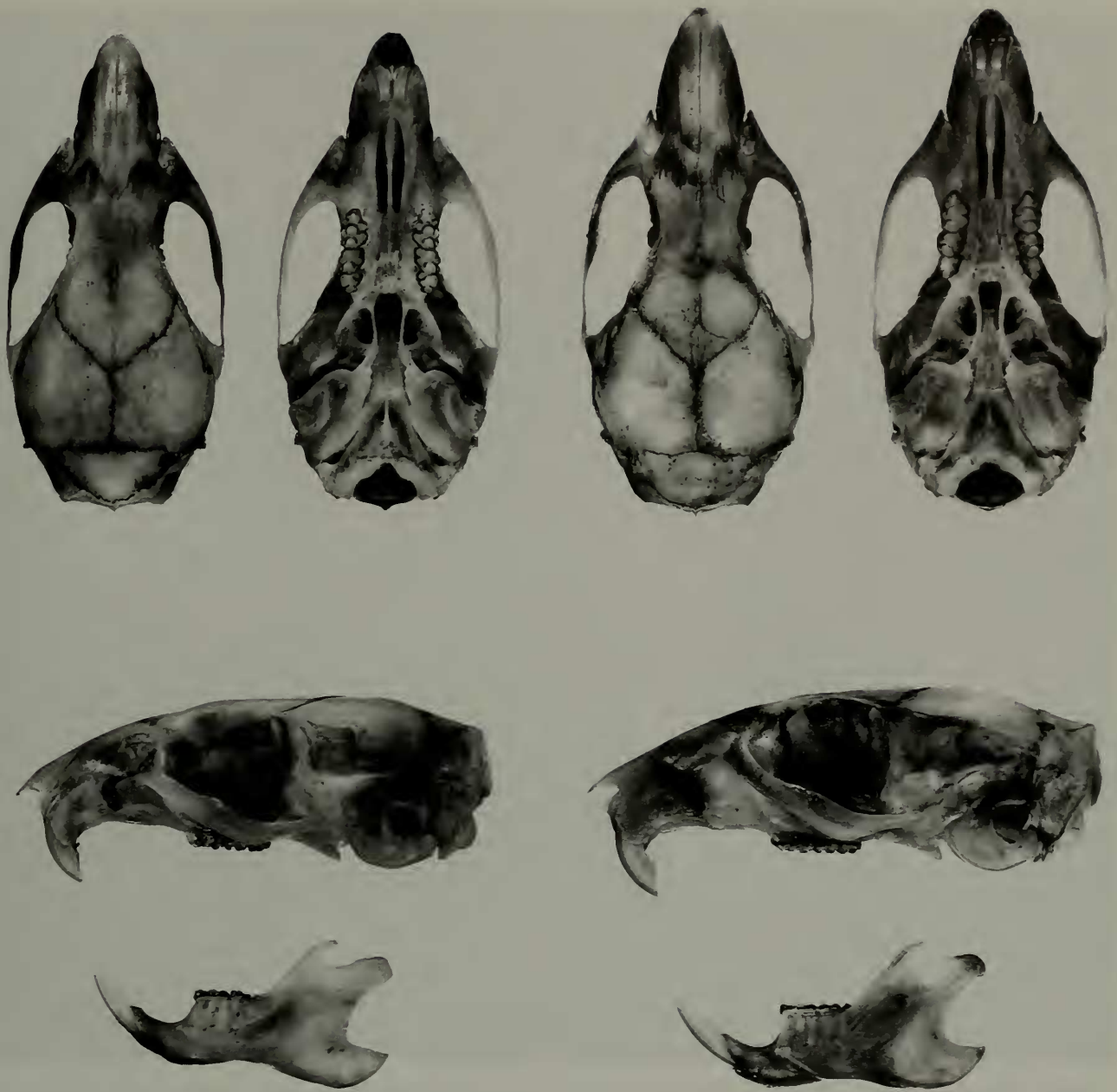


Fig. 8. Dorsal, ventral, and lateral views of crania and mandibles of young adult *Lemniscomys* (both Age Class 2): left, *L. zebra* (USNM 465402), a female from Burkina Faso, 6 mi SE Seguenega; and right, *L. barbarus* (USNM 475145), a male from from Morocco, 15 km E Agadir.

now at hand, but these are presented only as average differences or general impressions. Higher numbers of dorsal stripes appear more common within Subsaharan populations, which usually exhibit five, occasionally six, pairs of primary dark and light bands on either side of the mediodorsal line; in contrast, specimens from Northwest Africa possess four or five countable pairs of primary dark and light stripes. The impression of more dorsal stripes among Subsaharan series is visually accentuated by the development of secondary light lines,

which usually subdivide the first as well as the second primary dark stripes (Figs. 9B, D); within samples from northwestern Africa, secondary light lines are typically evident only within the first primary dark stripes, obscurely defined in the second and those more laterad (Fig. 9A). A pattern consisting of a broad, black vertebral line, bordered by more consolidated dark stripes and irregularly defined secondary light stripes (Fig. 9C), occurs more often among population samples from East Africa (the source of taxa such as *zebra*, *spekei*, and *nubalis*);



Fig. 9. Variation in dorsal pelage pattern of four specimens of striped grass mice, the *Lemniscomys barbarus* species group. A. *L. barbarus* (USNM 475121, LHB = 108 mm), a male from Morocco, 17 km SW Rabat. B. *L. zebra* (BMNH 23.5.12.81, LHB = 86 mm), a female from Niger, Farak (region of *olga* Thomas & Hinton 1921). C. *L. zebra* (USNM 165191, LHB = 89 mm), a female from Uganda, Rhino Camp (region of nominate *zebra* Heuglin 1864). D. *L. zebra* (USNM 376535, LHB = 88 mm), a male from Senegal, Kotiare Naoudé (region of *oweni* Thomas 1911).

a finely streaked dorsum (vertebral stripe narrower and secondary light stripes well delineated within the first and second primary dark bands) is typical of West African populations (taxa such as *nigeriae* and *oweni*—Fig. 9D).

With regard to the degree of pelage saturation, we observe a subtle trend toward paler, diluted upperparts in examples from more xeric vegetation zones. This association is best evidenced by the many USNM

examples from West Africa, wherein a darker pelage tone characterizes those specimens obtained from localities within Guinea savanna compared to the slightly paler aspect of series collected within Sudan savanna. At the darker extreme, somewhat muted colors and subdued contrast mark the dorsum of Moroccan populations (Fig. 9A) that occupy the relatively mesic Mediterranean region of Northwest Africa; at the pallid end of this spectrum are the few

specimens (Fig. 9B), including the holotype of *olga*, that originate from the Sahel zone in West Africa.

As a generality, specimens of the *L. barbarus* group possess moderately hispid dorsal fur, especially over the rump, compared to those of the *L. striatus* complex. Within the *L. barbarus* group, most taxa, as represented by their type specimens, generally conform in this trait with the exception of the more hispid condition characteristic of *olga*.

### Discussion

*Taxonomic conclusions.*—The major pattern of craniodental variation uncovered here provides evidence for the specific divergence of the Moroccan samples from those representing populations that occur to the south of the Sahara Desert. The former correspond to *Lemniscomys barbarus* s.s. (Linnaeus 1766), and the oldest name applicable to the latter is *L. zebra* (Heuglin 1864), whose type locality lies in southern Sudan. Seven of our 11 OTUs were regrettably coarsely defined in geographic coverage, an analytical approach dictated by the generally small sample sizes available from the majority of collecting localities. Notwithstanding the composite nature of most OTUs, we believe that the regions thus broadly sampled are sufficient to sustain the principal taxonomic conclusion recommended here—the recognition of north-west African populations (*L. barbarus*) as a species distinct from those occupying savanna biomes in West and East Africa (*L. zebra*).

Intraspecific taxonomic uncertainties persist, however, within the Subsaharan moiety we identify as *L. zebra*, as intimated by the appreciable size and chromatic variation observed among those samples. The earlier conclusions of Robert T. Hatt of the American Museum illustrate the biological problems inherent in understanding that variation. In his reports (Hatt 1935, 1940) on the rodents collected by the AMNH Congo Ex-

pedition (1909–1915), Hatt provided diagnostic criteria for three “natural groups” of the *L. barbarus* group that originated from a single locality, Faradje. Hatt identified the three as separate species—*L. zebra*, *L. dunnii nubalis*, and *L. oweni orientalis*, the last newly described as a “dwarf” subspecies of West African *oweni*. For us, unambiguous, repeatable separation of East African specimens into discrete species using Hatt’s identification criteria remains elusive. The mensural diagnostic values (means?) listed by Hatt for each “species”—for instance, foot length, 25 versus 25 versus 23 mm; greatest skull length, 27.5 versus 27.2 versus 26.7 mm; length upper molar row, 4.8 versus 5.1 versus 4.6 mm—span the normal variational spectrum that we find within population and regional samples (Appendix 2). Unfortunately, Hatt provided no measures of sample dispersion nor gave any attention to potential age effects for the numerical contrasts offered, statistical precautions now standardly addressed when evaluating intersample mean differences. The pelage attributes given (general color, spiciness, and facial stripes) are subjective to apply precisely and suggest no variation between individuals from large series, which contradicts our experience. Within the Faradje material, it is notable that Hatt allocated the two “pallid, very hispid” individuals to *L. dunnii nubalis* (named from central Sudan) and the remainder of the “dark, hispid” specimens, totaling 17, to either *L. zebra* or *L. oweni orientalis*, the latter two separable by average size. Darker versus paler pelage hues and hispid versus very hispid fur are traits whose expression appears subject to slight variation within locality series and to clinal trends over broad regions, for example, Guinea through Sahel savannas in West Africa. In view of the geographic location of Faradje near the southern limit of Guinea savanna in eastcentral Africa, one might anticipate that the majority of specimens would appear relatively dark and moderately hispid.

In summary, we interpret the differences



tabulated by Hatt (1935, 1940) as examples of intraspecific variation of the one species, *L. zebra*, not sympatry of three members of the *L. barbarus* group. In the same papers, Hatt (1935:1–2) previewed this possibility:

“That a more conservative person or one with a greater series of specimens than have been available to me might lump all three as fortuitous variations of a single subspecies, I readily admit, but such a procedure would, . . . with the present evidence, but mask the simple assortment of characters as they have presented themselves and tend to smother rather than encourage further investigation of the problem of speciation or, it may be ecologic differentiation, in this region.”

His was a reasoned and reasonable taxonomic viewpoint, given the state of knowledge about African striped mice in the 1930s. From our vantage point of the late 20th century, and hoping to “encourage further investigation,” we draw attention to three alpha-systematic problems not yet adequately resolved by the Sub-Saharan material at our disposal.

For one, the nature of morphological differentiation between East (*zebra*) and West African (*oweni*) populations should be further appraised drawing upon other kinds of data and improved geographic sampling (Chad and the Central African Republic are apparently unrepresented in museum collections). For example, another sibling species pair of *Lemniscomys*, *L. macculus* and *L. bellieri* of the *striatus* group, is distributed as East and West African counterparts (Van der Straeten 1975, Van der Straeten & Verheyen 1979, 1980). Some geographic integrity of East versus West African examples of striped grass mice is suggested by the phenetic clusters generated from craniodontal similarity, but the segregation is not complete: one West African sample (Senegal, OTU 3) groups among East African OTUs, and another from East Africa (Kenya, OTU 11) aligns with those from West Africa (Fig. 6). In light of such ambiguous results, set against the inadequacy of geographic coverage and the apparent want of other diagnostic traits, we prefer at

this investigatory stage to retain all Sub-Saharan populations, except *L. hoogstraali* (see below), under the one species *L. zebra* (Heuglin 1864) without formal delineation of geographic races.

For another, the taxonomic status of Thomas & Hinton's (1921) *olga* merits reexamination. The form, described from a few specimens and fewer localities in Sahel Savanna in southcentral Niger, is characterized by small size, pale color, finely delineated striping pattern (Fig. 9B), and slightly more hispid pelage texture. The three specimens from Timbuktu, Mali, another locality in the Sahel, also recall this morphology. In view of the type specimen's morphometric association with other West African populations (Fig. 7), and while acknowledging the distinctiveness of the form's pelage and habitat, retention of *olga* as a junior synonym of *L. zebra* seems prudent as a provisional arrangement. Careful geographic transects across Sudan and Sahel woodlands, both in West and East Africa, are required to illuminate the nature of morphological variation in characters attributed to *olga* and critically judge its taxonomic status.

The third species of the *Lemniscomys barbarus* complex herein recognized, *L. hoogstraali*, was described by Dieterlen (1991) from the Upper Nile Province of southern Sudan (Figs. 1, 12). As noted by Dieterlen, the form contrasts with neighboring Sudanese examples of *L. barbarus* (= *L. zebra* as here understood) by its larger external and cranial size and by the dorsal striping pattern (see additional commentary under Taxonomic Accounts). The dark stripes of the upperparts are exceptionally black and broad, which, together with the purity of the primary white stripes and indistinct secondary white stripes, heightens the alternating, zebra-like effect of the holotype (and only known specimen). Such an appearance is suggested, as an extreme of pelage variation, by some individuals from East Africa (see Fig. 9C), but their cranial measurements otherwise fit those recorded

Table 4.—Selected cranial dimensions (as measured by Van der Straeten) of thirteen type specimens of species-group taxa assigned to the *Lemniscomys barbarus* group. All taxa listed are viewed as junior synonyms of *L. zebra*, except *ifniensis*, allocated to *L. barbarus* (Linnaeus 1766), and *hoogstraali*, retained as a third species of the group.

Taxon & authorship (type)	Age class	Variables									
		ONL	ZB	BBC	IOB	LN	LIF	LD	BMI <sub>s</sub>	BZP	ALM
<i>zebra</i> Heuglin, 1864 (SMNS 1100a/5422)	1–2	26.7	12.8	11.7	4.5	10.0	5.0	6.0	5.3	3.5	5.30
<i>spekei</i> De Winton, 1897 (BMNH 63.7.7.23)	3	29.3	13.6	12.3	4.5	11.1	5.5	6.7	6.4	3.9	5.75
<i>dunni</i> Thomas, 1903 (BMNH 3.2.8.15)	5	27.8	—	12.0	4.3	10.4	5.7	6.3	5.7	3.7	5.70
<i>albolineatus</i> Osgood, 1910 (FMNH 17194)	3	27.5	13.0	12.5	4.3	10.4	5.7	6.3	5.8	3.3	5.45
<i>convictus</i> Osgood, 1910 (FMNH 17206)	4–5	29.9	13.8	12.1	4.5	11.5	5.9	6.7	5.9	3.7	5.35
<i>oweni</i> Thomas, 1911 (BMNH 11.6.10.61)	2–3	27.0	12.5	11.4	4.3	10.3	5.5	6.3	—	3.2	5.25
<i>manteufeli</i> Matschie, 1911 (BZM 16025)	1	26.7	13.0	11.9	4.3	9.1	5.2	5.9	5.2	2.9	5.10
<i>nigeriae</i> Thomas, 1912 (BMNH 12.1.16.45)	5	29.1	13.1	11.7	4.9	11.1	5.7	6.9	6.0	3.7	5.55
<i>olga</i> Thomas & Hinton, 1921 (BMNH 21.2.11.128)	2	27.1	12.8	11.7	4.3	10.5	5.1	6.1	5.8	3.5	5.50
<i>nubalis</i> Thomas & Hinton, 1923 (BMNH 18.7.2.14)	4	29.2	—	12.1	4.5	11.5	6.0	6.9	6.1	4.0	5.60
<i>orientalis</i> Hatt, 1935 (AMNH 49626)	5	26.8	12.5	11.4	4.1	10.1	5.7	6.3	5.5	3.2	5.00
<i>ifniensis</i> Morales A., 1935 (MNCN 9638)	6	31.3	14.3	13.0	4.9	12.5	6.4	7.4	6.3	3.9	5.35
<i>hoogstraali</i> Dieterlen, 1991 (USNM 342078)	5–6	32.0	—	12.8	5.0	12.5	6.1	7.5	6.5	4.0	5.75

for eastern series of *L. zebra* and are clearly smaller than the holotype of *L. hoogstraali* (Table 4). In dimensions of the skull and molars alone, the type of *L. hoogstraali* instead agrees with those of *L. barbarus* proper from Morocco (Table 4, Appendix 2). Although based on a single specimen, the combination of large size and dramatically striped dorsum, considered with the form's geographic occurrence approximate to typical examples of *L. zebra*, leads us to accept Dieterlen's (1991) judgement of *hoogstraali* as a species. Additional samples should be sought in order to enhance appreciation of its variation, phyletic relationships, and level of differentiation from *L. barbarus* and *L. zebra*.

With revision of the striped grass mice, there now exists a basic framework of spe-

cies definitions and their distributional limits within *Lemniscomys*, a moderately diverse genus embracing at least 11 species associated in three groups: namely, *barbarus* (*barbarus*, *hoogstraali*, and *zebra*), *griselda* (*griselda*, *linulus*, *rosalia*, and *roseveari*), and *striatus* (*bellieri*, *macculus*, *midendorfi*, and *striatus*). Future systematic attention should focus on phylogenetic relationships among the species and the evidence for accepting these nominal groupings as monophyletic. While visually obvious and thus advantageous for employment in taxonomic keys, the dorsal pelage patterns that have traditionally afforded definition of the species groups of *Lemniscomys* may not necessarily convey phyletic affinity. Although readily distinctive as represented by the typical species of each

group, these basic striping configurations are not necessarily so well defined among all of a group's members. Some individuals of West African *L. linulus*, for instance, exhibit indistinct lateral spotting in addition to the pronounced middorsal stripe, a pattern reminiscent of the upperparts of some *L. bellieri*. For another example, the Nigerian form *fasciatus*, now synonymized under *L. striatus* (see Van der Straeten & Verheyen 1980), was long confused with *L. barbarus* (now = *L. zebra*) as a result of the nearly continuous union of its lateral spots.

In contrast to their external dissimilarity, one is impressed by the fundamental craniodental resemblance among the species of *Lemniscomys*. Certain morphological traits may further characterize these groups, at least as exemplified by their typical species. Examples of *L. barbarus* possess well inflated ectotympanic bullae relative to those of *L. griselda* (intermediate) and *L. striatus* (smallest); the degree of inflation may correspond to the openness of the habitats occupied by each species. The molars of *L. griselda* are broad and robust compared to those of *L. barbarus* and especially *L. striatus*. Along with its heavier, more rounded cusps, the t3 of M1 in *L. griselda* is weakly defined and the t9 appears as a short spur off t8; the t3 of M2 is minute and irregularly formed. The cheekteeth of *L. striatus* seem more cuspidate, with the t3 of M1 separated from t2 by a distinct cleft and the t9 formed as a small albeit discrete cusp apart from t8; the t3 of M2 is small but consistently formed. In general, the molars of *L. barbarus* more closely resemble those of *L. griselda*. Such observations should be extended to the other species of *Lemniscomys* and additional morphological characters sought in order to test the monophyly of the currently defined species groups.

Investigation of chromosomal homologies promises to shed light on kinship groups within *Lemniscomys*, as suggested by the karyotypic differences so far reported. Based on a single specimen from Algeria, Filippucci et al. (1987) reported the

diploid number (2N) of *L. barbarus* as 54 and the number of autosomal arms (AN) as 58, dominated by a graded series of 23 small to large acrocentric pairs, along with two pairs of small metacentrics and one large submetacentric pair. This diploid count agrees with those reported for *L. zebra* from Burkina Faso (Gautun et al. 1986, as *L. barbarus*), Ivory Coast (Matthey 1954, also as *L. barbarus*), and from Cameroun (Van der Straeten, pers. com.); the Cameroun animals even display the same fundamental number (AN = 58), although having three pairs of small metacentrics and apparently lacking the large submetacentric pair. These chromosomal traits appreciably differ from karyotypes that Van der Straeten & Verheyen (1978) documented for Ivory Coast samples of *L. bellieri* (2N = 56) and of *L. striatus* (2N = 44). Such preliminary results should be reconfirmed and extended to include other species, and their differences and mechanism of karyotypic change explored with the banding techniques now available.

*Distributions and zoogeographic implications.*—Museum specimens of *L. barbarus* and *L. zebra* have originated from habitats that can be loosely categorized as savanna, woodland, or scrubland. All such places, in general, have ample grass and/or herbaceous ground cover intermingled with bushes to small trees, but never close-canopied, high forest. Nonetheless, the vegetational character where each species occurs can be broadly contrasted.

On skin tags and in field catalogs, collectors in West Africa have recorded the vegetation of almost all trapping sites of *L. zebra* as either Guinea or Sudan savanna (or woodland), following Rosevear's (1953, 1965) terminology. To date, only a handful of specimens come from the Sahel, but few collections have been made in this very arid zone. These vegetational associations differ in their dominant plant species, physiognomy of the low-canopied woods, and density of ground cover, features which in turn correspond to amount of annual rainfall,

length of dry season, and prevailing lowest relative humidity (Guinea savanna, more mesic, to Sahel savanna, more arid). To the east, areas where striped grass mice live have been characterized as grass and scrub (Uganda—Delany 1975), drier savannas and steppes (East Africa—Kingdom 1974), or simply as savanna (annotations on USNM skin tags of Sudanese specimens collected by H. W. Setzer). Our localities from Sudan, Zaire, and Uganda also lie within vegetation zones mapped by Rosevear (1953, 1965) as Guinea, Sudan, or Sahel savanna.

At Zizonkame, about 8° north latitude in Benin (Fig. 10, Top), degraded Guinea savanna contained prolific grasses three to four feet high, periodically burned, as well as some cultivated plots (cassava) and oil palms (field notes of J. W. LeDuc and C. B. Robbins, USNM Mammal Division archives). Here, individuals of *L. zebra* were obtained with a variety of small mammals, including: *Atelerix albiventris*, *Galago senegalensis*, *Xerus erythropus*, *Thryonomys swinderianus*, *Tatera* sp., *Taterillus gracilis*, *Cricetomys gambianus*, *Arvicanthis niloticus*, *Dasymys rufulus*, *Lemniscomys striatus*, *Mastomys natalensis*, *Myomys daltoni*, *Mus musculoides*, and *Uranomys ruddi*. In the vicinity of Cella, about 11°30' north latitude in Burkina Faso (Fig. 10, Bottom), examples of *L. zebra* were trapped amongst dry grasses that formed a uniform ground cover, interspersed with shrubs and low-canopied trees, which together composed a plant community typical of Sudan savanna. The less diverse set of small mammals collected at this site included: *Atelerix albiventris*, *Galago senegalensis*, *Tatera* sp., *Taterillus gracilis*, *Steatomys pratensis*, *Arvicanthis niloticus*, and *Mastomys natalensis*. Populations of *L. zebra* and *L. striatus* were found to co-occur at the locality within Guinea savanna, but only examples of *L. zebra* were collected in the drier Sudan savanna.

Populations of *L. barbarus* also inhabit various nonforested, relatively dry habitats,

but along the coastal region and contiguous low plateaus of Northwest Africa, where the severity of drought is moderated by the Atlantic Ocean and Mediterranean Sea. In Morocco, notations on specimen tags identify collecting places as “rocky outcrop in vegetated coastal dunes,” “coastal scrub,” “sandy hummocks with dense vegetation,” “juniper scrub,” “argon-sage-grassland,” and “argon savanna.” Such Moroccan locales denote a spectrum of climatic domains classified as arid, semiarid, or even humid (see fig. 6 in Saint Girons & Petter 1965: 18).

At two places along the valley of the Souss River in Agadir Province, Morocco (about 30°30' north latitude), specimens of *L. barbarus* were obtained with those of *Atelerix algirus*, *Gerbillus* sp., *Gerbillus hoogstraali*, *Meriones shawi*, *Mastomys erythroleucus*, and *Mus spretus*. The collector, R. E. Vaden, described the site at 16 km W Aoulouz (Fig. 11, Top) as “more coastal type of vegetation . . . predominantly argon trees and grass . . . clumps of assorted shrubs, from sage through thorn-bushes (acacia?) up to small argons, maximum of about 6 feet in height . . . in between [shrubby clumps], it's grassy.” The locality at 5 km S Taroudannt (Fig. 11, Bottom), he characterized as “heavily-vegetated sandy dune area . . . dominant shrubs are the same thorny bushes seen all along . . . some sage, but not like the last camp [16 km W Aoulouz]—relatively smaller . . . plenty of grass both under the shrubs and in the open areas” (R. E. Vaden field notes, USNM Mammal Division). At the latter site, samples of *L. barbarus* were captured in the grassy areas.

The regional distributions of *L. zebra* and *L. barbarus* do concord with previously recognized biogeographic subregions of Africa, as distilled from both plant and animal studies (Chapin 1932; Moreau 1952, 1966; Rosevear 1953, 1965; Davis 1962; Brenan 1978; Quézal 1978; Rautenbach 1978; Crowe & Crowe 1982; see Skinner & Smithers 1990:xxii, for their helpful map

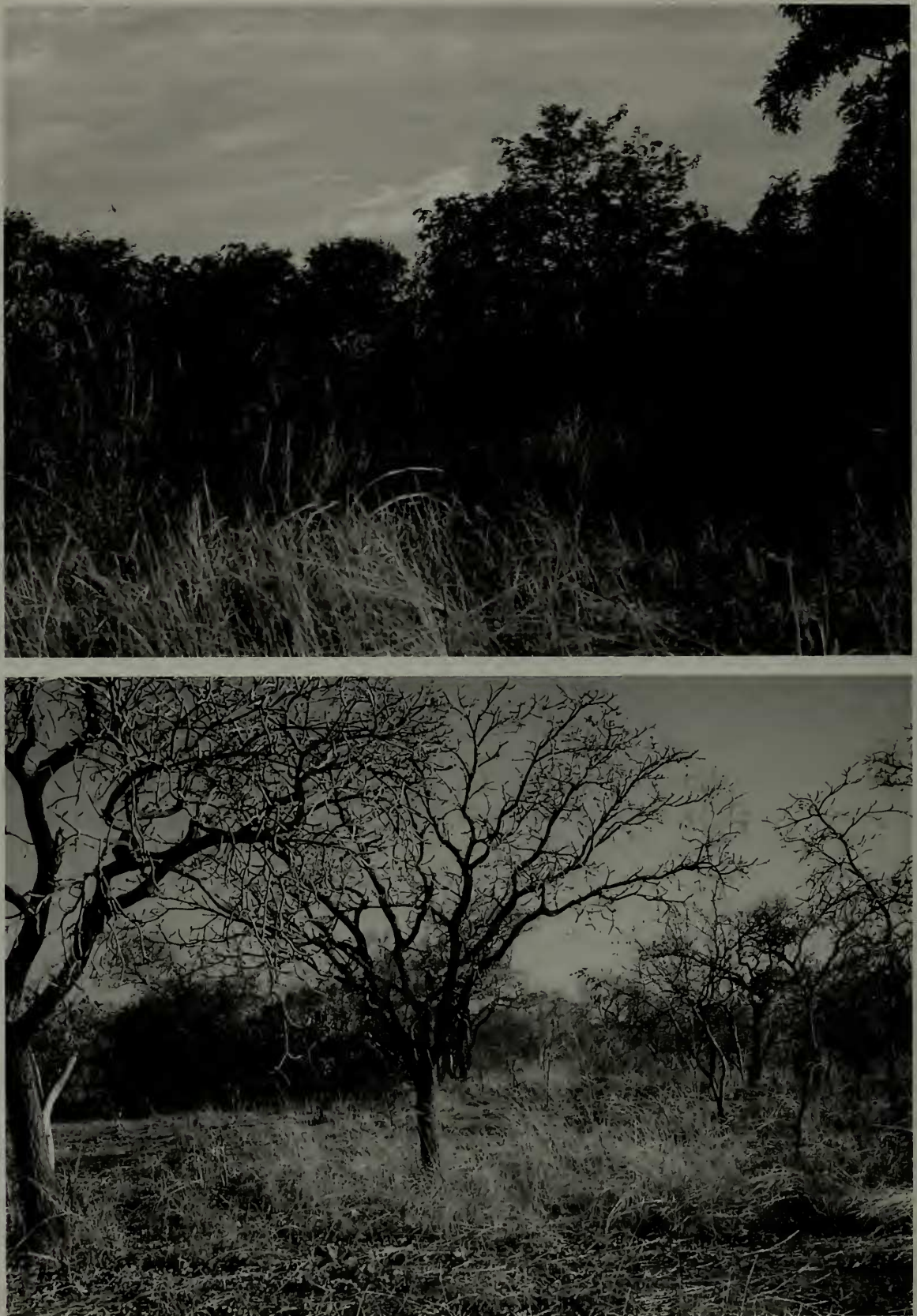


Fig. 10. Two examples of West African vegetation inhabited by populations of *Lemniscomys zebra*. Top, degraded Guinea Savanna in the vicinity of Zizonkame ( $07^{\circ}55'N$ ,  $02^{\circ}01'E$ ), Benin, in the early rainy season (middle April); examples of both *L. striatus* and *L. zebra* were captured here. Photograph by James W. LeDuc. Bottom, Sudan Savanna in the vicinity of Cella ( $11^{\circ}38'N$ ,  $00^{\circ}22'W$ ), Burkina Faso, in the late dry season (middle March); only specimens of *L. zebra* were trapped here. Photograph by Robert E. Vaden.

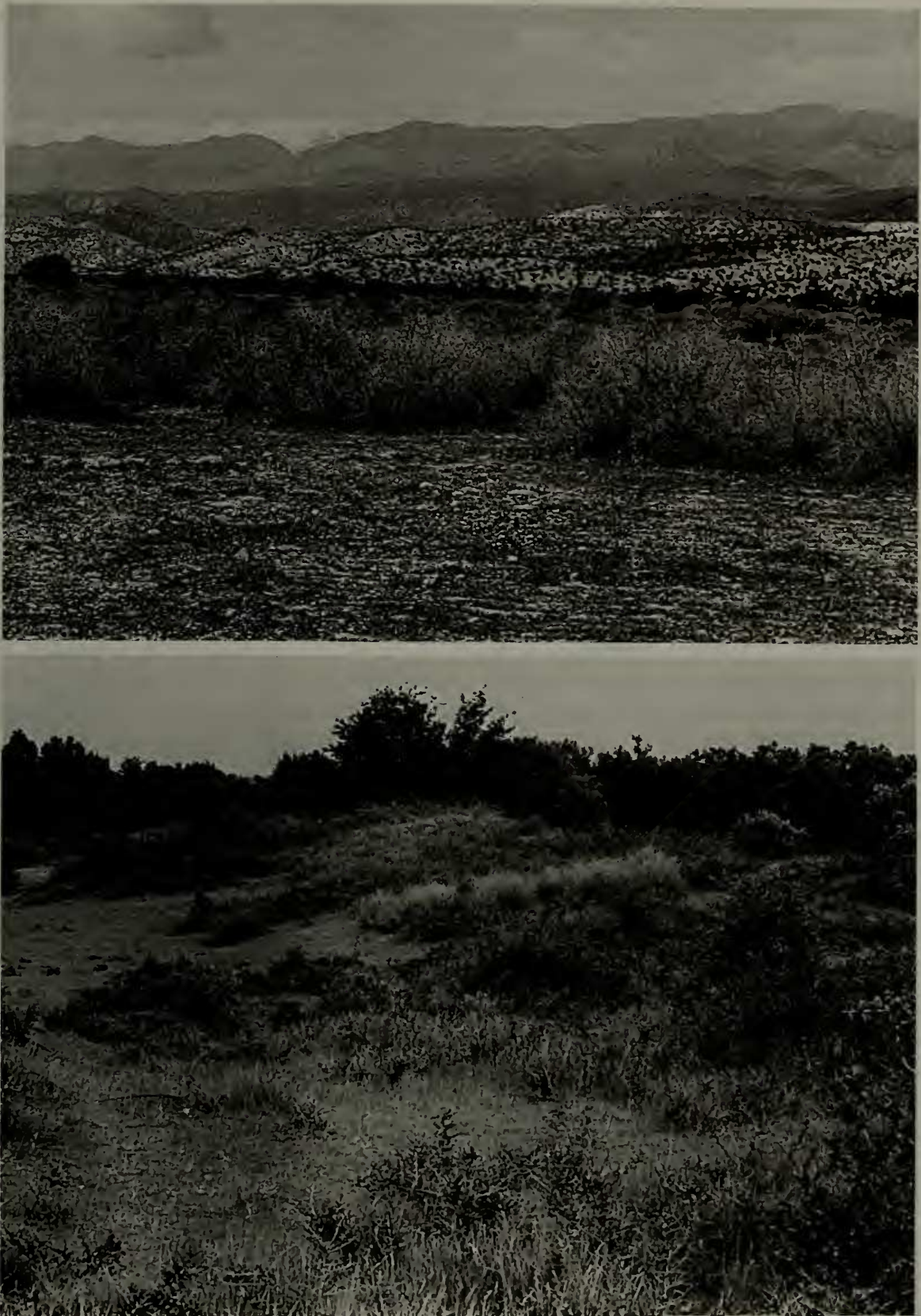


Fig. 11. Two examples of Moroccan coastal vegetation inhabited by populations of *Lemniscomys barbarus*. Top, mixed argon-sage-grassland at 16 km W Aoulouz ( $30^{\circ}42'N$ ,  $08^{\circ}18'W$ ), Agadir Province; snow covered peaks of the High Atlas Mountains are visible in the left background. Bottom, heavily vegetated dunes with thorny shrubs, dense brush, and grasses at 5 km S Taroudannt ( $30^{\circ}26'N$ ,  $08^{\circ}54'W$ ), Agadir Province; samples of *L. barbarus* were mainly collected in the grassy areas. Photographs by Robert E. Vaden.

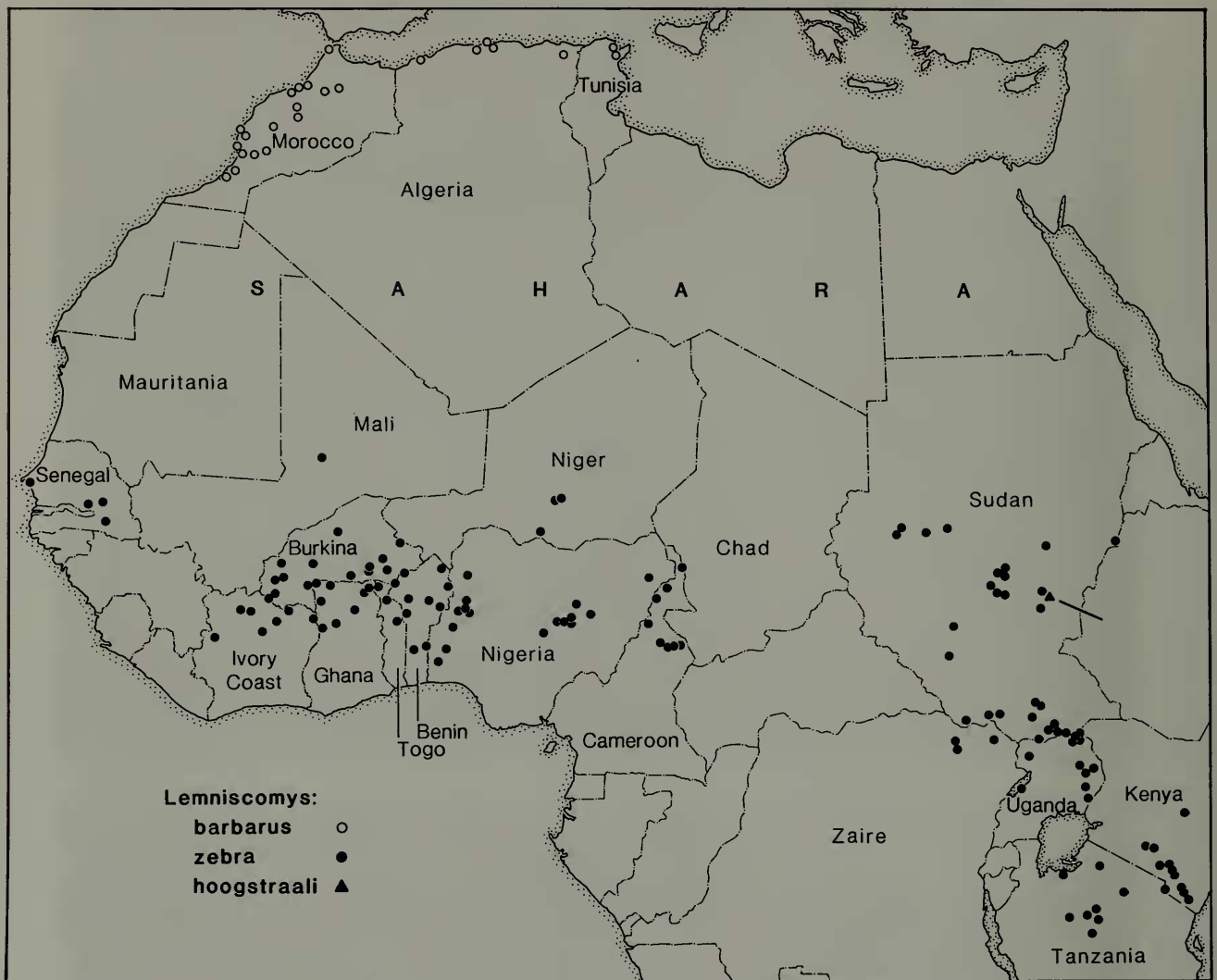


Fig. 12. Distribution map of African striped mice of the *Lemniscomys barbarus* species group, based on 649 specimens examined by the authors (see Taxonomic Accounts) from 177 principal collecting localities (see Appendix 1).

and tabular comparison of biotic classifications). Although the formal names adopted for ecophysical subdivisions may differ, particularly between plant and animal investigations, the principal areas (whether called subregions, zones, districts, domains, etc.) are remarkably complementary across these several works on African biogeography. For the present discussion, we employ the terminology formulated by Davis (1962) for Ethiopian Africa, as modeled after the earlier avifaunal studies of Chapin (1932) and Moreau (1952), with the addition of a Barbarian province as delineated by Heim de Balsac (1936), Moreau (1952), and Quézal (1978, called Mediterranean-Northern African Domain).

Museum specimens of *L. zebra* vouch its

occurrence across a swath of savanna biotopes to the south of the Sahara Desert, from Senegal to central Sudan and southwards to southern Kenya and northcentral Tanzania (Fig. 12). These localities are virtually coterminous with three biotic zones within tropical Africa that have been designated as Sudanese Arid (Sahel and Sudan Savannas of Rosevear 1953), Northern Savanna (Guinea Savanna of Rosevear 1953), and Somali Arid. At the western terminus of its distribution in Senegal, *L. zebra* does not enter the Sahara Desert proper (not present in USNM series from Mauritania). The abrupt southward projection of its range in Benin and western Nigeria (The Dahomey Gap), almost to the Gulf of Guinea, conforms to the anthropogenic prolif-

eration of invasive Guinea savanna (Booth 1958, Robbins 1978). At its eastern limits, the extension of *L. zebra* into Kenya and Tanzania follows an arid tract of acacia steppe called the Somali Arid Zone. Although this eastern African region of relatively high endemism shares species also native to either northern or southern savanna biomes (Moreau 1966, Brenan 1978, Coe & Skinner 1993), it displays a slightly stronger biogeographic affinity with the Southern Savanna Zone based on nonforest bird distributions (Crowe & Crowe 1982). However, as so far known, populations of *L. zebra* do not inhabit any part of the Southern Savanna Zone (Davis 1962, Rautenbach 1978—including both his Southern Savanna Woodland and Southern Savanna Grassland), whose northernmost extent reaches western Tanzania (see map in Skinner & Smithers 1990:xxii).

Locality records of *L. barbarus* outline a comparatively restricted distribution that adheres to the coastal sectors of Morocco, Algeria, and Tunisia and is bounded by the upper elevations of the Atlas Mountains (Fig. 12). In Morocco, its distribution covers the coastal lowlands and the contiguous Central Plateau, extending inland only to the northern and northwestern foothills of the Anti Atlas, High Atlas, and Middle Atlas Mountains (also see Aulagnier & Thevenot 1986:80). USNM locality records for Morocco document an altitudinal range from sea level to about 750 m, as interpolated from topographic maps. In Algeria and Tunisia, the species occurs mainly along the narrow Mediterranean coastal strip but also among the folded ridges of the Tell Atlas, low mountains which closely approach the seacoast (and see Bernard 1969:109, and Kowalski & Rzebik-Kowalska 1991:257).

Biogeographers have previously recognized the area inhabited by *Lemniscomys barbarus* as the Barbarian Zone (Heim de Balsac 1936, Moreau 1952), a biological island isolated on the north and west by the Atlantic Ocean and Mediterranean Sea and

on the south and east by the Sahara Desert, which reaches the coastline in Mauritania and in Libya. The northwest rim of the African continent, by virtue of its maritime geological setting coupled with climatic oscillations of the Plio-Pleistocene and accompanying vegetational shifts, has formed a mixing bowl for species spreading from Afrotropical, European, and Asian landscapes. Indeed, the high diversity and striking endemism recorded for plants and animals of the area bear testimony to its refugial character and recurring opportunity for taxonomic differentiation (Heim de Balsac 1936, Moreau 1966, Quézal 1978, Cheylan 1990).

Although the Barbarian Zone today harbors a predominance of temperately adapted species of Palearctic affinities, Heim de Balsac (1936) had regarded the majority of mammals living there as having Ethiopian origins. Such an interpretation contrasted to the large Palearctic contingent observed among the avifauna, an apparent zoogeographic anomaly expanded by Moreau (1966). However, Heim de Balsac had conflated under his "Indo-Ethiopian" category not only broadly distributed paleotropical mammals (many carnivores) but also xeric-adapted species occurring across the deserts of the Sahara, Arabian Peninsula, and Middle East. The many gerbilline rodents numbering among the latter prejudice the interpretation of Moroccan mammals as predominantly "Ethiopian" sensu Heim de Balsac. Subsequent biogeographic studies of Barbarian mammals have supported their substantial Palearctic pedigree (Saint Girons & Petter 1965, Agustí 1989, Aulagnier 1990, Cheylan 1990, Kowalski & Rzebik-Kowalska 1991), a finding concordant with the broad picture of Northwest African biodiversity as disclosed by other organisms (Moreau 1966, Quézal 1978). Still, the mosaic of tropical and temperate habitats long offered within the Barbarian region has fostered some isolation and differentiation of Subsaharan groups, and Linnaeus' Barbary Mouse, *Lemniscomys barbarus*, represents



Table 5.—Rodent species<sup>a</sup> indigenous to the Barbarian Zone<sup>b</sup> of Northwest Africa, with indication of their biogeographic affinity or probable origin.

Taxon (* = endemic)	Ethiopian	Palearctic	
		European	Saharo-Sindean
Sciuridae			
<i>Atlantoxerus getulus</i> *	X		
<i>Xerus erythropus</i>	X		
Muridae: Gerbillinae			
<i>Gerbillus campestris</i>			X
<i>Gerbillus hesperinus</i> *			X
<i>Gerbillus hoogstraali</i> *			X
<i>Gerbillus jamesi</i> *			X
<i>Gerbillus maghrebi</i> *			X
<i>Gerbillus occiduus</i> *			X
<i>Meriones shawi</i>			X
Muridae: Murinae			
<i>Apodemus sylvaticus</i>		X	
<i>Lemniscomys barbarus</i> *	X		
<i>Mastomys erythroleucus</i>	X		
<i>Mus spretus</i>		X	
Myoxidae			
<i>Eliomys melanurus</i>		X	
Dipodidae			
<i>Jaculus orientalis</i>			X
Hystricidae			
<i>Hystrix cristata</i>	X?		
Totals	5	3	8

<sup>a</sup> Species compiled from systematic reviews of mammals for Morocco (Aulagnier & Thevenot 1986; Saint Girons & Petter 1965), Algeria (Kowalski & Rzebik-Kowalska 1991), and Tunisia (Bernard 1969), with the taxonomy updated to accord with Wilson & Reeder (1993).

<sup>b</sup> The limits of the Barbarian Zone have been variously defined, but are here understood to include the coastal lowlands of Morocco, Algeria, and Tunisia, the inland high plateaus, and the Atlas Mountains (for example, per Quézal 1978). Such a regional definition thus excludes typical desertic formations of the Sahara and, correspondingly, many rodents, especially gerbills.

another of these endemics, one of the few rodent species plausibly derived from Afrotropical (Ethiopian) relatives (Table 5). Other rodent species with satellite populations in Northwest Africa similarly merit re-

newed study of their differentiation and taxonomic status (for example, *Apodemus sylvaticus*, *Mastomys erythroleucus*, many species of *Gerbillus*, *Meriones shawi*, and *Eliomys melanurus*).

The historical biogeography of Africa's savanna landscapes has received less attention in contrast to that devoted to forest-dwelling vertebrates and their patterns of distribution, species diversity, and endemism (for example: Moreau 1966, Crowe & Crowe 1982, Carleton & Robbins 1985, Grubb 1990, and references cited by each). Nevertheless, biotic affinities among savanna biomes, as currently delimited and understood, provide sufficient insight to frame a series of hypotheses to explore the evolutionary diversification of species of *Lemniscomys*.

1.—Are single-striped mice (*griseldarosalia-roseveari*), largely confined to the Southern Savanna Zone, the sister group to the *striatus* and *barbarus* complexes of northern savannas and woodlands? That is, does possession of multiple stripes, arranged either in continuous (*barbarus* group) or in punctulated lateral lines (*striatus* group), form a synapomorphy for those more northern mice? Is *L. linulus*, a single-striped form isolated in far West Africa (Van der Straeten 1980a), the vicariant sister species to *L. griselda* and its kin in the Southern Savanna Zone, or does the former represent an instance of evolutionary convergence, having been derived from a *striatus*-like ancestor through suppression of lateral striping?

2.—If the *striatus* group (distribution centered in Guinea savanna) and *barbarus* group (more common in Sudan vegetation) are so closely related, how can one explain their divergence? Other studies have divulged little support for the latitudinally graded, contiguous savanna bands found south of the Sahara Desert as refugia or centers of endemism (Moreau 1966, Brenan 1978). Evidence from ornithological diversity and centers of endemism (Crowe & Crowe 1982), however, provides some sup-

port for a nonforest refugium in eastern equatorial Africa (within the contemporary Somali Arid Zone), where the progenitor of one complex (*striatus*?) may have differentiated in isolation from the other (*barbarus*?) in arid habitats fringing the Sahara, before secondary contact and distributional overlap.

3.—The autochthonous origin of *L. barbarus* in the Barbarian Zone is parsimoniously explained as allopatric speciation after final severance (late Pliocene–early Pleistocene?) from Subsaharan populations (ancestral to *L. zebra*) along the West African coast. The ranges of other Afrotropical species with apparently conspecific segments in southern Morocco similarly intimate former connection (*Xerus erythropus*) or document present continuity (*Acomys cahirhinus*, *Mastomys erythroleucus*) of populations across this westernmost region. Although reasonable as a first explanation, caution is advised, for yet other corridors of contact with Subsaharan Africa may have existed during pluvial intervals of the Pleistocene: for example, via the highlands that occur through the middle of the Saharan Desert or along the eastern Mediterranean coast (Quézal 1978). In either case, determining the nearest kinship of *L. hoogstraali* (eastcentral Sudan) and the status of East versus West African moieties of *L. zebra* will assume importance in understanding the evolutionary derivation of *L. barbarus*.

Such phylogenetic questions and their geographic scale elegantly lend themselves to investigation using genetic sequencing and phylogenetic reconstruction (for example, see Matthee & Robinson 1997, on the springhare, *Pedetes*).

#### Taxonomic Accounts

*Lemniscomys barbarus* (Linnaeus 1766)

*Mus barbarus* Linnaeus, 1766: unpaginated addenda at end of volume (type locality, “Barbaria” = Morocco).—Trouessart, 1881:124.

*Arvicanthis barbarus*, Trouessart, 1897: 498.—Trouessart, 1904:388.

*Lemniscomys barbarus*, Thomas, 1916:68 (subsequent designation as type species).—Cabrera, 1921:58.—Misonne, 1974: 20 (part).—Honacki et al., 1982:520 (part).—Aulagnier & Thevenot, 1986:80 (part).—Le Berre, 1990:276 (part).—Corbet & Hill, 1991:180 (part).—Musser & Carleton, 1993:601 (part).

*Lemniscomys barbarus barbarus*, Cabrera: 1932:272.—Allen, 1939:391.—Ellerman, 1941:131.—Saint Girons & Petter, 1965: 37.—Kowalski & Rzebik-Kowalska, 1991:259.

*Lemniscomys barbarus ifniensis* Morales Agacino, 1935:390 (type locality, Spanish Morocco [Morocco], Sidi Ifni, Ifni; holotype—MNCN 9638).—Allen, 1939: 391.—Ellerman, 1941:131.—Saint Girons & Petter, 1965:37.—Misonne, 1974: 20 (listed in synonymy without indication of rank).—Aulagnier & Thevenot, 1986: 80 (listed in synonymy without indication of rank).—Le Berre, 1990:276 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

*Emended diagnosis*.—A species of *Lemniscomys* characterized by longitudinally continuous dorsal stripes; upperparts generally more muted in tone, alternating dark and light stripes less sharply contrasting due to suffusion of ochraceous over middle dorsum; primary dark stripes on either side of mediadorsal line typically four in number, fifth stripe absent or indistinct; secondary light line usually present and continuous within first lateral dark stripe, incomplete or poorly defined in second lateral dark stripe; size relatively large and skull robustly developed, as observed in adult dimensions of both the body (total length > 235 mm) and cranium (occipitonasal length > 29.0 mm; zygomatic breadth > 13.5 mm).

*Distribution*.—Coastal region of Morocco, Algeria, and Tunisia, northwest and

north of the Atlas Mountains (Fig. 12). Other locality records based on owl-pellet recoveries or reliable sightings of *L. barbarus* have been reported for Morocco (Aulagnier & Thevenot 1986), Algeria (Kowalski & Rzebik-Kowalska 1991), and Tunisia (Bernard 1969), but these sites do not alter the general picture of distribution as documented by the specimens we examined and enumerate below.

*Remarks.*—Although some specimens used by Linnaeus in his *Systema Naturae* still exist and may be regarded as types (see Addendum on *L. striatus*), Van der Straeten has searched unsuccessfully for a likely type of *Mus barbarus* in the Naturhistoriska Riksmuseet, Stockholm, and the museum of the University of Uppsala, Sweden. Since *L. barbarus* is the only species of *Lemniscomys* isolated in northwest Africa, wholly allopatric to other congeners, identification poses no problems and restriction of the type locality to some place other than “Barbaria,” regarded as equivalent to Morocco (Allen 1939, Ellerman 1941), is unwarranted at this time.

*Specimens examined.*—124, as follows.

Algeria: Alger (BMNH 12.3.12.144–12.3.12.151, 19.7.7.1952; BZM 1664; MNHN 1975.117); Hammam Meskoutine (BMNH 20.7.19.51); Hammam Rirha (BMNH 12.6.12.152–12.6.12.155); Oran (ZMA 8653, 8654; MNHN 1953.830–1953.832, 1955.618, 1955.619, 1961.894, 1961.1063); Reghaia (MAKB 54.111, 54.112). Algeria, locality unknown (BMNH 44.50, 44.51, 19.7.7.1952, MNHN 1956.616).

Morocco: Enzel (BMNH 98.7.4.29); Forêt de Néfifik (MNHN 1957.499, 1958.248); 31.5 km on road from Marrakesh to Casablanca (MNCN 9657-9659); 15 km WNW Marrakesh (SMF 47.781); Meknès (MNHN 1964.377); Oued Sebo (BMNH 76.1077); Oued Cherrat (ZMA 4834). Agadir Province, 8 km S Tiznit (USNM 475125); 15 km E Agadir (USNM 475126–475148); 16 km W Aoulouz (USNM 475150–475164); 5 km S Taroudannt (USNM 475165–

475168); 8 km N Tamri (USNM 475169). Khouribga Province, 5 km S Oued Zem (CM 45286; USNM 475170–475182). Rabat Province, 17 km SW Rabat (USNM 475121, 475122). Safi Province, 13 km E Essaouira (USNM 475123, 475124); 15 km SW Rabat (USNM 475149); 5 km NE Essaouira (USNM 482104, 483092–483094). Sidi Ifni Province, Ifni (MNCN 9638). Tanger Province, 3 km S Cap Spartel (USNM 475183); Tanger (MNCN 9654). Morocco, locality unknown (MNCN 9655, 9660, 9661; MNHN 1950.405, 1950.407, 1950.872).

Tunisia: Algeriet (NHRS M810); Cédria (Potinville) (MAKB 71.210–71.214); La Marsa (MAKB 71.215).

*Lemniscomys hoogstraali* Dieterlen, 1991

*Lemniscomys hoogstraali* Dieterlen, 1991: 11 (type locality, Sudan, Upper Nile Province, 12 miles N Niayok, Paloich, about 10°22'N–32°33'E; holotype, USNM 342078).—Musser & Carleton, 1993: 601.

*Emended diagnosis.*—Linear markings of upperparts sharply contrasted, the primary dark stripes wide and black, offset by narrower, almost white primary light stripes; secondary light stripes weakly expressed and incomplete, hence primary dark stripes undivided; size of skull closely similar to *L. barbarus*, notably larger relative to *L. zebra*.

*Distribution.*—Known only from the type locality in eastern Sudan (Figs. 1, 12).

*Remarks.*—Dieterlen (1991:11) diagnosed this new form as a “Large species of the *Lemniscomys barbarus* group. Tail length small (101% of head and body length); dorsal coloration rich in contrast and with broad blackish stripes; skull relatively large; incisive foramina ending anterior to M<sup>1</sup>; zygomatic plate indented below.” However, the discriminatory value of several of these traits is unhelpful when compared to large series of *L. barbarus* and *L. zebra*. Many specimens of the latter two species have the forward edge of their zy-

gomatic plate undercut ventrally. In fact, the protuberance of the anterodorsal edge of the plate typically becomes accentuated in older specimens, and, as noted by Dieterlen, the holotype of *L. hoogstraali* is an old individual (age class 5–6). Similarly, the absolute and relative length of the incisive foramina is foreshortened in older individuals of *L. barbarus*, just meeting the anterior roots of the first molar instead of extending conspicuously between them. Contrary to Dieterlen's assertion that *L. hoogstraali* exceeds even *L. barbarus* sensu stricto in cranial size, the measurements of the holotype are typical of old adult specimens of *L. barbarus* and fall within the variational limits recorded for our Moroccan samples (Table 4, Appendix 2). Finally, the terminal caudal segment of the holotype's skin appears missing, which may partially account for the exceptional shortness (101%) of its relative tail length (proportion of TL/HBL ranges from 115 to 123% in samples of *L. barbarus* and *L. zebra*—Appendix 2).

Notwithstanding the caveats attached to certain diagnostic features advanced by Dieterlen, we concur with his naming of the specimen as a new species. Although similar to *L. hoogstraali* in cranial size, no specimen of true *L. barbarus* exhibits such strongly delineated upperparts and broad, richly black stripes. Furthermore, the robust size of *L. hoogstraali*, as judged by both hindfoot length (28 mm) and most cranial dimensions (Table 4), is certainly greater than any surrounding Sudanese examples of *L. zebra*. And while some skins of East African *L. zebra* may approach the consolidated striping evident in *L. hoogstraali*, none that we have seen quite matches it. More and larger series must be assembled to rigorously evaluate the characters and status of Dieterlen's new form, so far known only by the holotype, its condition imperfect (tail tip missing; skull with both zygoma incomplete, right bulla crushed, and pterygoid processes broken off).

*Specimens examined*.—1, the holotype.

Sudan: Upper Nile Province, 12 miles N Niayok, Paloich (USNM 342078).

*Lemniscomys zebra* (Heuglin 1864)

- Mus zebra* Heuglin, 1864:10 (type locality, Bahr el Ghazal [Sudan], "Lande der Req-Neger, Djur und Bongo;" lectotype, SMNS 1100a).—Trouessart, 1881:124.
- Arvicanthis zebra*, Trouessart, 1897:499.—Trouessart, 1904:388.
- Arvicanthis barbarus zebra*, Osgood, 1910:10.
- Lemniscomys barbarus zebra*, Hollister, 1919:144.—Allen, 1939:392.—Hatt, 1940:511.—Ellerman, 1941:131.—Setzer, 1956:511.—Kingdon, 1974:620.—Missonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys zebra*, Kershaw, 1924b:25.
- Arvicanthis spekei* De Winton, 1897:318 (type locality, Tanganyika Territory [Tanzania], Unyamuezi; holotype, BMNH 63.7.7.23).—Trouessart, 1904:388.
- Arvicanthis barbarus spekei*, Osgood, 1910:10.
- Lemniscomys barbarus spekei*, Matschie, 1911:338.—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Missonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Arvicanthis dunni* Thomas, 1903:297 (type locality, Western Kordofan [Sudan], Kaga Hills, about 120 mi [193 km] W El Obeid; holotype, BMNH 3.2.8.15).—Trouessart, 1904:388.
- Lemniscomys dunni dunni*, Allen, 1939:392.—Setzer, 1956:512.
- Lemniscomys barbarus dunni*, Ellerman, 1941:131.—Dekeyser, 1955:204.—Missonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Arvicanthis barbarus convictus* Osgood,

- 1910:10 (type locality, British East Africa [Kenya], Voi; holotype, FMNH 17206).
- Lemniscomys barbarus convictus*, Hollister, 1919:146.—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Arvicanthis barbarus albolineatus* Osgood, 1910:11 (type locality, British East Africa [Kenya], Ulukenia Hills, Lukenya Mountain; holotype, FMNH 17194).
- Lemniscomys barbarus albolineatus*, Hollister, 1919:144.—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys albolineatus*, Kershaw, 1924a:536.
- Arvicanthis oweni* Thomas, 1911b:120 (type locality—French Gambia [Senegal], upper Gambia River, Gemenjulla, 50 ft [15 m]; holotype, BMNH 11.6.10.61).
- Lemniscomys oweni oweni*, Allen, 1939:394.
- Lemniscomys barbarus oweni*, Ellerman, 1941:131.—Dekeyser, 1955:204.—Rosevear, 1969:336.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys barbarus manteufeli* Matschie, 1911:338 (type locality, Tanganyika Territory [Tanzania], south coast of Lake Victoria, Mwanza; holotype, BZM 16025).—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Arvicanthis barbarus nigeriae* Thomas, 1912:272 (Nigeria, Panyam, 4000 ft [1220 m]; holotype, BMNH 12.1.16.45).
- Lemniscomys barbarus nigeriae*, Allen, 1939:391.—Ellerman, 1941:131.—Rosevear, 1953:102.—Dekeyser, 1955:204.—Rosevear, 1969:336.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys olga* Thomas & Hinton, 1921:9 (type locality, Damergou [Niger], Takoukout, 1550 ft [472 m], about 15°N and 09°E; holotype, BMNH 21.2.11.128).—Ellerman, 1941:131.—Dekeyser, 1955:204.
- Lemniscomys dunni olga*, Allen, 1939:392.
- Lemniscomys barbarus olga*, Rosevear, 1969:335.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys dunni nubalis* Thomas & Hinton, 1923:267 (type locality, Southern Kordofan [Sudan], Nuba Country, Talodi, 1300 ft [396 m]; holotype, BMNH 18.7.2.14).—Allen, 1939:392.—Hatt, 1935:1; 1940:513.—Setzer, 1956:512.
- Lemniscomys barbarus nubalis*, Ellerman, 1941:131.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Lemniscomys oweni orientalis* Hatt, 1935:2 (type locality, Belgian Congo [Zaire], Faradje; holotype, AMNH 49626).—Allen, 1939:391.—Hatt, 1940:513.
- Lemniscomys barbarus orientalis*, Ellerman, 1941:131.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).
- Emended diagnosis.*—A species of *Lemniscomys* characterized by longitudinally continuous dorsal stripes; upperparts generally brighter, alternation of dark and light stripes better defined compared to *L. barbarus*; primary dark stripes on either side

of mediodorsal line typically five in number, with secondary light lines usually present and continuous within first and second dark laterals; external and cranial size medium and skull moderate in build (total length < 230 mm; occipitonasal length < 29.0 mm; zygomatic breadth < 13.5 mm).

*Distribution.*—Grassy woodlands and savannas south of the Sahara Desert, from Senegal in the west to southern Sudan in the east, southwards through northeasternmost Zaire, northern Uganda and western Kenya, to northcentral Tanzania (Fig. 12); altitudinal range from near sea level to 1220 m in West Africa (Panyam, Nigeria) and to 1065 m in East Africa (north of Dodoma, Tanzania).

*Remarks.*—Heuglin (1864) did not indicate a type specimen for *Mus zebra*, a common omission for the period, nor is his text clear about the number of specimens available when he described the new species. During his visits (in 1979, 1983, and 1989) to the Staatliches Museum für Naturkunde, Stuttgart (SMNS), Van der Straeten located two specimens of *Lemniscomys* that bear evidence of association with Heuglin's original description, a mounted skin and skull (SMNS 1100a) and a complete specimen in alcohol (SMNS 1100b). Labels attached to the mounted skin and fluid specimen each contain the information "Bongo; Von Heuglin, 1865," and the notation as type, the last datum obviously appended more recently. Heuglin's original characterization of the new form provides little help, for it only mentions coloration, pattern of stripes, and external measurements, all of which could have been plausibly derived from either a whole mount or a fluid-preserved carcass, or from both. He did note that he was not yet able to examine the molars, which admission suggests that the skull had not been cleaned (Heuglin provided cranial measurements for other species described in the same paper). Both Stuttgart specimens are currently listed as a "Holotypus" of *Lemniscomys barbarus zebra* in the SMNS card catalog (Fritz Dieterlen, personal com-

munication), but they should be properly regarded as syntypes of Heuglin's (1864) *Mus zebra*.

The fully mounted skin with cleaned skull, however, is more useful for ascertaining diagnostic traits of the form, and we designate this specimen (SMNS 1100a) as lectotype of *Mus zebra* Heuglin (1864). The fluid specimen (SMNS 1100b) becomes the de facto paralectotype of the binomen (see Recommendation 73F, International Code of Zoological Nomenclature, Third Edition, 1985). The skin is mounted in a more or less realistic posture, and its label indicates male, but the sex cannot be confirmed by inspection of the skin. Although faded, presumably from years of museum exhibit, the mounted skin clearly displays the alternating dark and light (six to seven) dorsal stripes typical of the dorsal pelage of the *barbarus* group. Associated with the skull is an older but now invalid museum number, "Skelett-Katalog 5422," an extraneous number dating from the outmoded practice of assigning separate registrations to osteological and skin preparations, even for the same individual. The light molar wear (age class 1-2) suggests a young, perhaps immature, animal. Except for slight breakage of the pterygoid processes and mandibular rami, the skull of the lectotype is otherwise intact and in good condition. According to a posteriori probabilities of membership derived from discriminant function analysis, specimen number SMNS 1100a predictably intermingles with other Subsaharan samples that we identify as *L. zebra* (Fig. 7); in particular, the lectotype was marginally classified ( $P = 0.45$ ) with specimens from Zaire (OTU 8), a group assignment likely due to its young age and correspondingly smaller size as compared to most Sudanese examples used in our analyses.

The form *Arvicanthis fasciatus* Wroughton (1906), named from southern Nigeria and occasionally listed as a subspecies of *L. barbarus* (Allen 1939, Rosevear 1969), was reidentified as a synonym of *L. striatus* by Van der Straeten & Verheyen (1980).

Rosevear (1969:333) erred in listing the type locality of *L. olga* Thomas & Hinton (1921) as Farniso, Nigeria, and citing the type specimen as BMNH 21.2.11.87. Van der Straeten has not been able to locate this specimen in the BMNH; the type locality (Niger, Takoukout) and registration number (BMNH 21.2.11.128) given in our synonymy agree both with the authors' original publication and with the provenience as written on the skin tag of the holotype.

Although *L. zebra* probably occurs in westernmost Ethiopia, Yalden's et al. (1996) report of its presence (as *L. barbarus*) at Arba Minch is questionable. Rupp (1980) had allocated these specimens (SMNS 16751, 16754), both young individuals, to *L. striatus* but also confided his difficulty in discerning the striping configuration as typical of that of *striatus* or of *barbarus*. The damaged condition of their skins and skulls precludes exact determination, but Van der Straeten tentatively refers the two specimens to *L. macculus* based on their smaller auditory bullae as determined from his subsequent examination in 1983.

*Specimens examined*.—524, as follows.

Benin: Atacora Region, Kouande (USNM 439584, 439585); Porga (USNM 439586); Soubroukou (USNM 439582, 439583). Borgou Region, Bimbereke (USNM 422058–422060); Guene (USNM 422061, 422062); Nikki (USNM 422081–422084); Segbana (USNM 422063–422080). Central Region, Diho (USNM 422057); Zizonkame (USNM 439580, 439581). Benin, locality unknown (MNHN 1913.13).

Burkina Faso: Arly (USNM 450853, 450854); 5 mi N Boussouma (USNM 465401); 6 mi S Cella (USNM 465404, 465405); 1 km N Cella (USNM 465406–465410); Djipologo (USNM 466682–466684); Fo (USNM 466674–466679); 5 km SW Koutoura (USNM 466681); Nasso (RUCA 1278, 1281–1283, 1289, 1345–1347, 1349–1356, 1370–1380, 1393–1398, 1414–1416, 1459, 1470, A.1–A.9, A.12–A.15); Natiaboani (USNM 450855); 3 km SE Nayoure (USNM 465411); Nian-

goloko (BEL 13243); 9 mi S Nobere (USNM 450852); 27 km ENE Orodara (USNM 466680); Ougarou (USNM 465412); Oulo (USNM 465413, 465414); 6 mi SE Seguenega (USNM 465402, 465403).

Cameroun: Boukma (RUCA 2.134); Fort Foureau (MNHN 1956.678); 35 km S Garoua (AMNH 241233); 35 km S and 10 km E Garoua (CM 58903, 58905, 58909); Isiri (RUCA 1087); Kali (RUCA 1098, 1099, 1114); Koum (RUCA 1018, 1066, 1095, 1122); Maroua, 20 km NW Dogba (CM 14975, 14978); Mora (MAKB 73.393–73.395, 73.397, 73.398); Sir (RUCA 1.479, 1.482, 1.492, 1.549, 1.591, 1.592, 1.595).

Ghana: Damango (USNM 466694–466697). Eastern Region, Legon, Accra Plains (USNM 412745–412747). Northern Region, Gambaga (USNM 435405); Nabogo (USNM 435400–435402); Sakpa (USNM 420577–420585). Upper Region, Bangwon (USNM 420573–420576); Piri (USNM 420570); Pulima (USNM 420571, 420572); Shishe (USNM 435403, 435404).

Ivory Coast: Bambela (BEL 13177, 13178); Bandama, near Tiebila (FMNH 105180); Bouna (BEL 3798; MNHN 1971.757, 1971.758); Kafiné (BEL 13695); Kong (USNM 465398–465400); Ouango Fitini (BEL 3802, 3932, 13902, 13903, 13931, 13945, 13949, 13984, 23354, 23368, 23373, 23375, 23377, 23379–23382); Tyenko (USNM 466685–466687); Yama (USNM 466688–466693).

Kenya: Garissa District, Galma Galla, 270 ft (AMNH 187678, 187679); Machakos District, Kathekani, 760 m (CM 102462, 102463); Kilabasi (AMNH 114445); Voi District, Kenya Karanzi (AMNH 114446); Machakos District, Kiboko, 3100 ft (USNM 437394); Machakos District, 11 km N and 17 km E Kibwezi (CM 98258); Machakos (BMNH 34.10.26.11, 34.10.26.12); Maungu (CM 57977); Masi, Sand River (AMNH 114449); 50 mi S Moctow (AMNH 114447, 114448); Mtoto Andei (USNM 181737–181740); near Tana River (MCZ

16222); Taveta (BMNH 10.7.2.115); Ulukenia Hills, Athi Plains (USNM 162884); Ulukenia Hills, Lukenya Mountain (FMNH 17194); Voi (BMNH 10.6.2.125, 29.3.17.167; FMNH 17206).

Mali: Timbuktu (FMNH 44713; ZMK 3885, 3886).

Niger: Farak, 1475 ft (BMNH 25.5.12.80, 25.5.12.81, 39.2083, 39.2084); Gerari (Tessawa) (BMNH 25.5.12.83); Takoukout (BMNH 21.2.11.128).

Nigeria: Bauchi (BMNH 68.491); Borgu (HAP 1318, 1322); Dada (USNM 404085–404087); Igbo Ora (USNM 404041); Kabwir (BMNH 12.9.10.3, 13.5.2.3, 13.5.2.4, 14.11.8.3); 1 mi S Kabwir (USNM 375975); Kishi (HAP 1026); Mada River, 3 mi E Gudi (USNM 404043); 22 mi S Maiduguri, Bornu Ranch (USNM 379011-6); New Bussa (HAP 1068, 1069, 1073); Panyam, 4000 ft (BMNH 12.1.16.42–12.1.16.47, 12.4.3.34, 12.4.3.36); Panyam Fish Farm, 2 mi N Panyam, Jos Plateau (USNM 404020–404040, 404044–404084); Shangunu (USNM 379647); Upper Ogun Ranch, 12 mi N Iseyin (USNM 404042); Wawa (HAP 901, 938, 943, 1778, 1779); Yankari (HAP 1106); Zaria (HAP 585).

Senegal: Bandia (MAKB 76.269); Gemenjulla (BMNH 11.6.10.61, 11.6.10.63–11.6.10.67); Kotiare Naoude, 27 km NE Tambacounda (USNM 376533–376536); Koussanar (USNM 376529–376532).

Sudan: Agur (BMNH 28.3.11.51, 28.3.11.52); Badigeru Swamp, 20 mi E Mongalla (BMNH 20.4.26.22); Bahr el Zeraf (MAKB 27–30); Bahr al Ghazal (BMNH 17.10.4.18); Bongo (SMNS 1100a, 1100b); Delami (BMNH 29.5.19.26); Duk Majok (BMNH 8.4.2.41, 8.4.2.42); El Fasher (BMNH 23.1.1.302, 23.1.1.303, 23.1.1.305); Fashoda (BMNH 1.8.8.26); Gallabat (BMNH 28.1.11.151); Gondokoro (USNM 165192); Ikoto, 2500 ft (USNM 299764; ZMK 11942, 11944, 11947); Imurok (ZMK 11934–11937); Juga Juga (BMNH 20.7.30.18); Kadugli (SMF 33.218); Kaga Hills, about 120 mi W El Obeid (BMNH 3.2.8.15); Nuba

Mountains, G. Koalib, Kudring (BMNH 29.5.19.27; FMNH 35313, 35314); Kuna (BMNH 23.1.1.308); Li Rangu (USNM 318003); Loa (ZMK 14084); Maridi (SMNS 27396); Molongori (ZMK 14096); Nimule, 1800 ft (FMNH 67293; USNM 299771); Nile-Congo watershed (BMNH 21.1.8.7); Nuba Mountains (BMNH 18.7.2.16); Tadoro (SMF 33.217); Talodi, 1300 ft (BMNH 18.7.2.13, 18.7.2.14); Terrakekka (BMNH 28.3.11.53); Torit, 2000 ft (FMNH 66853, 66854, 66857, 66859, 66860, 67171, 67172, 67175, 79500–79502; USNM 299765–299770; ZMK 14081–14083, 14088, 14092, 14100, 14104); 30 km W Torit (SMNS 27398, 27399, 27401, 27402); 80 km E Juba-Torit (SMNS 27397); Umm Keddada (BMNH 23.1.1.309, 23.1.1.311, 23.1.1.312). Southern Sudan, locality unknown (SMNS 27405, 27406).

Tanzania: Banagi (KBIN 15575); 50 mi N Dodoma, 3500 ft (CM 57782); Jumbe Kadala, Ussnoro (AMNH 55533; BMNH 24.1.1.180); Manyara Lake (BMNH 71.1246, 71.1247, 71.1249); Mawere (AMNH 83916–83920); Mdjengo's (BMNH 24.1.1.178, 24.1.1.179); Mtali's (MCZ 22958); Mwanza, south coast of Lake Victoria (BZM 16025); Ndogowe (BMNH 24.1.1.181); Pooma (MCZ 22957); Unyamuezi (BMNH 63.7.7.23).

Togo: Dapango (USNM 438311–438313); Paio (RUCA 551); Pewa (USNM 438314).

Uganda: Apeluk (BMNH 46.757–46.760); Apoka, Kidepo Valley National Park, Karamoja (BMNH 71.274); near Kaiso Valley, Bunyono (BMNH 71.277); west of road to Kananarock, Karamoja (BMNH 71.272); Karamoja (BMNH 71.273); Kidepo Valley National Park (BMNH 70.1065, 70.1066); near Loi Jome (AMNH 180121); Lorengikipi (AMNH 119166, 119169, 119170); south of Lorupei River crossing and post 18, Karamoja (BMNH 71.275, 71.276); Malera (BMNH 46.761); Nabilatuk (BMNH 63.928, 63.929); Nabumali (BMNH 67.900,



67.901); Rhino Camp, Lado Enclave (CM 850; USNM 165191, 165193, 165194, 165197, 165198, 165200–165205, 165422).

Zaire: Faradje (AMNH 49610–49615, 49617–49619, 49621–49633; KMMA 9040, 9191, 13015, 13016); Niangara (AMNH 49608, 49609); Tingasi (AMNH 2150).

#### Addendum on the Type of *Mus striatus* Linnaeus

Among the types housed by the Naturhistoriska Riksmuseet, Stockholm (NHRS), is a specimen of *Lemniscomys* that probably served as the basis of Linnaeus' (1758) description of *Mus striatus*, its habitat of origin then given as "India." In correcting the type locality of *striatus* to Sierra Leone, Thomas (1911a) did not remark on the existence of any original specimen, and as of 1969, Rosevear wrote that no type is known to exist. The preparation located by Van der Straeten in 1982 is a whole carcass (with skull still inside) preserved in alcohol. No formal registration number was associated with the fluid specimen, nor did Linnaeus mention any catalog number, per the non-standardized descriptive conventions of the earliest taxonomy. In a paper bag affixed to the bottle is an old label, upon which occurs the handwritten scientific name, "*Mus Striatus*," both in cursive and in printed letters; the number 48 appears on the outside of this bag. A newer label (one copy on the bottle and one inside with the specimen) contains the information: "*Mus striatus* Linne Typ. f.beshr.i.Mus. Ad Sp I.10 Syst Nat 10.62 Gamla saml. 48." This line provides the bibliographic essentials for the name: the reference to Linnaeus' original description that appeared in a publication (1754) of the Museum Regis Adophi Frederici, Volume I, page 10; and the *Systema Naturae*, 10th edition (1758), page 62, which references the former. Dr. Bo Fernholm, Department of Vertebrate Zoology, Naturhistoriska Riksmuseet, informed us

that "Gamla saml. is short for gamla samlingen and means Old Collection and refers to the fact that this specimen was # 48 of the old collection (i.e., before 1839) of the Royal Academy of Science, which was our mother institution until 1965 when the museum was separated as an independent government institution."

The small size and proportions of the specimen clearly indicate a juvenile animal. The sex of the immature individual appears to be male, although gender is not indicated on any tag. The pelage color seems diluted, perhaps from decades of leaching in old alcohol, and the stripes of the specimen immersed in fluid appear continuous. Nevertheless, seven pairs of dark and light punctulated stripes, distributed in the manner of *striatus*, are discernable on either side of the now brown (once black?) mediodorsal stripe when the specimen was removed from the jar and partially dried. The first through third light stripes exhibit distinctly separated spots, but the light markings of the fourth through seventh lines are set close together, suggesting an almost continuous effect. The belly is wholly white, like most *Lemniscomys*. Measurements obtained from the fluid specimen, as taken by Van der Straeten in 1982, include: length of head and body, 49.1 mm; tail length, 34.5 mm; hindfoot length, without claw, 13.4 mm. Its immaturity is underscored by comparison to these same dimensions in adult *L. s. striatus* from Ivory Coast, West Africa: length of head and body, 118.1 mm; tail length, 114.1 mm; hindfoot length, 26.0 mm (Van der Straeten & Verheyen 1978).

Troussart's (1881, 1898) early listings of *Mus striatus* supply circumstantial evidence that the Stockholm specimen is the one actually viewed by Linnaeus. That author indicated "*Mus striatus* L. (juv.)" as a synonym of *M. barbarus*, an interpretation consistent with the age and condition of the fluid specimen examined a century later by Van der Straeten. In the absence of any contrary evidence, this individual (NHRS A53.2048) in the Naturhistoriska Riksmu-

seet, Stockholm, should be considered the holotype of *Mus striatus* Linnaeus (1758) by reason of monotypy (see Article 73, International Code of Zoological Nomenclature, Third Edition, 1985).

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#### Literature Cited

- Aggundey, I. R., & D. A. Schlitter. 1984. Annotated checklist of the mammals of Kenya. I. Chiroptera.—*Annals of Carnegie Museum* 53:119–161.
- Agustí, J. 1989. On the peculiar distribution of some muroid taxa in the western Mediterranean.—*Bollettino della Società Paleontologica Italiana* 28:147–154.
- Allen, G. M. 1939. A checklist of African Mammals.—*Bulletin of the Museum of Comparative Zoology, Harvard* 83:1–763.
- Aulagnier, S. 1990. Zoogéographie et statut des carnivores sauvages du Maroc.—*Vie et Milieu* 40:150–155.
- , & M. Thevenot. 1986. Catalogue des mammifères sauvages du Maroc.—*Travaux de l'Institut Scientifique Cherifien, Série Zoologique* 41:163 pp.
- Bernard, J. 1969. Les mammifères de Tunisie et des régions voisines.—*Bulletin de la Faculté d'Agronomie* 24–25:41–172.
- Booth, A. M. 1958. The Niger, the Volta, and the Dahomey Gap as geographic barriers.—*Evolution* 12:48–62.
- Brenan, J. P. M. 1978. Some aspects of the phytogeography of tropical Africa.—*Annals of the Missouri Botanical Gardens* 65:437–478.
- Cabrera, A. 1921. Los Murinae de Marruecos.—*Boletín Real Sociedad Española de Historia Natural, special 50th Anniversary Volume*, pp. 42–58.
- . 1932. Los Mamíferos de Marruecos. Trabajos del Museo Nacional de Ciencias Naturales, Madrid, Serie Zoológica 57:361 pp.
- Carleton, M. D., & C. B. Robbins. 1985. On the status and affinities of *Hybomys planifrons* (Miller 1900) (Rodentia:Muridae).—*Proceedings of the Biological Society of Washington* 98:956–1003.
- , & C. Martinez. 1991. Morphometric differentiation among West African populations of the rodent genus *Dasymys* (Muroidea: Murinae), and its taxonomic implications.—*Proceedings of the Biological Society of Washington* 104:419–435.
- Chapin, J. P. 1932. The birds of the Belgian Congo. Part 1.—*Bulletin of the American Museum of Natural History* 65:756 pp.
- Cheylan, G. 1990. Endémisme et spéciation chez les Mammifères Méditerranéens.—*Vie et Milieu* 40:137–143.
- Coe, M. J., & J. D. Skinner. 1993. Connections, disjunctions, and endemism in the eastern and southern African mammal faunas.—*Transactions of the Royal Society of South Africa* 48:233–255.
- Corbet, G. B., & J. E. Hill. 1991. A world list of mammalian species, 3rd edition. Natural History Museum Publication, London, 243 pp.
- Crowe, T. M., & A. A. Crowe. 1982. Patterns of dis-

- tribution, diversity, and endemism in Afrotropical birds.—*Journal of Zoology* 198:417–442.
- Davis, D. H. S. 1962. Distribution patterns of South African Muridae, with notes on some of their fossil antecedents.—*Annals of the Cape Provincial Museums* 2:56–76.
- , & X. Misonne. 1964. Gazetteer of collecting localities of African rodents.—*Koninklijk Museum voor Midden-Afrika, Tervuren, Zoologische Documentatie* 7:1–100.
- Dekeyser, P. L. 1955. Les mammifères de l'Afrique Noire Française.—*Initiations Africaines, Institut Français d'Afrique Noire, Dakar* 1:426 pp.
- Delany, M. J. 1975. The Rodents of Uganda. British Museum (Natural History), London, 165 pp.
- De Winton, W. E. 1987. On a collection of small mammals from Uganda.—*Annals & Magazine of Natural History, London, series 6*, 20:316–320.
- Dieterlen, F. 1991. *Lemniscomys hoogstraali*, an new murid species from Sudan.—*Bonner Zoologische Beiträge* 42:11–15.
- Ellerman, J. R. 1941. The families and genera of living rodents. Volume 2, Family Muridae. London: British Museum (Natural History), 690 pp.
- Filippucci, M. G., M. V. Civitelli, & E. Capanna. 1987. The chromosomes of *Lemniscomys barbarus* (Rodentia, Muridae).—*Bollettino di Zoologia* 53:355–358.
- Gautun, J.-C., M. Tranier, & B. Sicard. 1986. Liste préliminaire des rongeurs du Burkina Faso (ex Haute-Volta).—*Mammalia* 49:537–542.
- Grubb, P. 1990. Primate geography in the Afro-tropical forest biome. Pp. 187–214 in G. Peters and R. Hutterer, eds., *Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn, 424 pp.
- Happold, D. C. D. 1987. The mammals of Nigeria. Oxford University Press, New York, 402 pp.
- Hatt, R. T. 1935. Taxonomic notes concerning arvicanthine rodents.—*American Museum Novitates* 790:4 pp.
- . 1940. Lagomorpha and Rodentia other than Sciuridae, Anomaluridae, and Idiuridae, collected by the American Museum Congo Expedition.—*Bulletin of the American Museum of Natural History* 76:457–604.
- Heim de Balsac, H. 1936. Biogéographie des mammifères et des oiseaux de l'Afrique du Nord.—*Bulletin Biologique de France et de Belgique, Supplément XXI*, 447 pp.
- Heuglin, Th. von. 1864. Beiträge zur Zoologie Central-Afrika's Leopoldina 31, Abhandlungen 7: 1–15.
- Hollister, N. 1919. East African mammals in the United States National Museum. Part II. Rodentia, Lagomorpha, and Tubulidentata.—*Bulletin of the United States National Museum* 99:184 pp.
- Honacki, J. H., K. E. Kinman, & J. W. Koepl. 1982. Mammalian species of the world. Association for Systematic Collections, Kansas, 641 pp.
- Kershaw, P. S. 1924a. On some small mammals from Tanganyika Territory.—*Annals & Magazine of Natural History, series 9*, 12:534–536.
- . 1924b. On two collections of mammals: (1) from Mongalla and Bahr-el-Ghazal, (2) from Lake Tsana, Abyssinia.—*Annals & Magazine of Natural History, series 9*, 13:19–29.
- Kingdon, J. 1974. East African Mammals. Volume II, Part B (Hares and Rodents): pp. 343–704. The University of Chicago Press, Chicago.
- Kowalski, K., & B. Rzebik-Kowalska. 1991. Mammals of Algeria. Ossolineum Publishing House, Wroclaw, Poland, 370 pp.
- Lamine Cheniti, T., & K. Sami. 1989. *Lemniscomys barbarus* (Rongeurs, Muridae), données biosystématiques et écologiques.—*Revue de la Faculté des Sciences Tunis, Série D*, 4:89–102.
- Le Berre, M. 1990. Faunes du Sahara. Volume 2. Mammifères. Lechevalier-R. Chabaud, Paris, 360 pp.
- Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 10th Edition. Volume 1. Laurentii Salvii, Stockholm, 824 pp.
- . 1766. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 12th Edition. Volume 1. Regnum Animale, part 1, pp. 1–532. Laurentii Salvii, Stockholm.
- Matschie, P. 1911. Über einige Säugetiere aus Muansa am Victoria-Nyansa.—*Sitzungs-Berichte der Gesellschaft naturforschender Freunde, Berlin* 8:333–343.
- Mathee, C. A., & T. J. Robinson. 1997. Mitochondrial DNA phylogeography and comparative cytogenetics of the springhare, *Pedetes capensis* (Mammalia: Rodentia).—*Journal of Mammalian Evolution* 4:53–73.
- Matthey, R. 1954. Nouvelles recherches sur les chromosomes des Muridae.—*Caryologia* 6:1–44.
- Misonne, X. 1974. Rodentia, main text. in J. Meester & H. W. Setzer, eds., *The mammals of Africa, an identification manual, Part 6*. Smithsonian Institution Press, Washington, D. C., 39 pp.
- Morales Agacino, E. 1935. Mamíferos de Ifni.—*Bolletín Sociedad Española de Historia Natural, Madrid* 35:381–393.
- Moreau, R. E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems.—*Proceedings of the Zoological Society of London* 121:869–913.
- . 1966. The bird faunas of Africa and its islands. Academic Press, New York, 424 pp.
- Musser, G. G., & M. D. Carleton. 1993. Family Muridae. Pp 501–755 in D. E. Wilson & D. M.

- Reeder, eds., Mammal species of the World, a taxonomic and geographic reference, Second Edition. Smithsonian Institution Press, Washington D. C., 1206 pp.
- Osgood, W. H. 1909. Revision of the mice of the American genus *Peromyscus*.—North American Fauna 28:1–285.
- . 1910. Diagnoses of new East African mammals, including a new genus of Muridae.—Field Museum of Natural History, Zoological Series, 10(2):5–13.
- Quézal, P. 1978. Analysis of the flora of Mediterranean and Saharan Africa.—Annals of the Missouri Botanical Gardens 65:479–534.
- Rautenbach, I. L. 1978. A numerical re-appraisal of the southern African biotic zones.—Bulletin of Carnegie Museum of Natural History 6:175–187.
- Robbins, C. B. 1978. The Dahomey Gap—a reevaluation of its significance as a faunal barrier to West African high forest mammals.—Bulletin of Carnegie Museum of Natural History 6:168–174.
- Rosevear, D. R. 1953. Checklist and atlas of Nigerian mammals, with a foreword on vegetation. The Government Printer, Lagos, Nigeria, 131 pp.
- . 1965. The bats of West Africa. British Museum (Natural History), London, 418 pp.
- . 1969. The rodents of West Africa. British Museum (Natural History), London, 604 pp.
- Rupp, H. 1980. Beiträge zur Systematik, Verbreitung und Ökologie äthiopischer Nagetiere. Ergebnisse mehrerer Forschungsreisen.—Säugetierkundliche Mitteilungen 28:81–123.
- Saint Girons, M.-C., & F. Petter. 1965. Les rongeurs du Maroc.—Travaux de l'Institut Scientifique Cherifien, Série Zoologique 31:1–58.
- Setzer, H. W. 1956. Mammals of the Anglo-Egyptian Sudan.—Proceedings of the United States National Museum 106:447–587.
- Skinner, J. D., & R. H. N. Smithers. 1990. The mammals of the southern African Subregion, Second Edition. University of Pretoria, South Africa, xxxii + 771 pp.
- Swynnerton, G. H., & R. W. Hayman. 1951. A checklist of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate.—Journal of the East Africa Natural History Society 20: 274–392.
- Thomas, M. R. O. 1903. On some mammals collected by Capt. H. N. Dunn, R. A. M. C., in the Sudan.—Proceedings of the Zoological Society of London 1903:294–301.
- . 1911a. The mammals of the Tenth Edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species.—Proceedings of the Zoological Society of London 1911:120–158.
- . 1911b. List of small mammals obtained by Mr. G. Fenwick Owen on the Upper Gambia and in Fouta Djallon.—Annals and Magazine of Natural History, London, series 8, 8:117–124.
- . 1912. Mammals of the Panyam Plateau, northern Nigeria. II.—Annals and Magazine of Natural History, London, series 8, 9:269–274.
- . 1916. On the rats usually included in the genus *Arvicanthis*.—Annals and Magazine of Natural History, London, series 8, 18:67–70.
- , & M. A. C. Hinton. 1921. Captain Angus Buchanan's Air Expedition. II. On the mammals (other than ruminants) obtained during the expedition to Air (Asben).—Novitates Zoologicae 28:1–13.
- , & ———. 1923. On the mammals obtained in Darfur by the Lynes-Lowe Expedition.—Proceedings of the Zoological Society of London 1923:247–271.
- Trouessart, E.-L. 1881. Catalogue des mammifères vivants et fossiles. Ordre des Rongeurs.—Bulletin de la Société d'Études Scientifiques d'Angers 10:58–212.
- . 1898–1899. Catalogus mammalium tam viventium quam fossilium. Volume 1. R. Friedländer & Sohn, Berlin, 664 pp.
- . 1904–1905. Catalogus mammalium tam viventium quam fossilium. R. Friedländer & Sohn, Berlin, 929 pp.
- Van der Straeten, E. 1975. *Lemniscomys bellieri*, a new species of Muridae from the Ivory Coast (Mammalia, Muridae).—Revue de Zoologie Africaine 89:906–908.
- . 1976. *Lemniscomys striatus dieterleni*, a new subspecies of Muridae from Zaïre (Mammalia, Muridae).—Revue de Zoologie Africaine 90: 431–434.
- . 1980a. Etude biométrique de *Lemniscomys linulus* (Afrique Occidentale) (Mammalia, Muridae).—Revue de Zoologie Africaine 94:185–201.
- . 1980b. A new species of *Lemniscomys* (Muridae) from Zambia.—Annals of the Cape Provincial Museums, Natural History, 13:55–62.
- . 1981. Note sur *Lemniscomys striatus venustus* (Thomas, 1911).—Mammalia 45:125–128.
- , & B. Van der Straeten-Harrie. 1977. Étude de la biométrie crânienne et répartition d'*Apodemus sylvaticus* et d'*A. flavicollis* en Belgique.—Acta Zoologica et Pathologica Antwerpiensia 69:169–182.
- , & W. N. Verheyen. 1978. Karyological and morphological comparisons of *Lemniscomys striatus* (Linnaeus, 1758) and *Lemniscomys bellieri* Van der Straeten, 1975, from Ivory Coast (Mammalia:Muridae).—Bulletin of Carnegie Museum of Natural History 6:41–47.
- , & ———. 1979. Note sur la position systé-

- matique de *Lemniscomys macculus* (Thomas et Wroughton 1910) (Mammalia, Muridae).—Mammalia 43:377–389.
- , & ———. 1980. Relations biométriques dans le groupe spécifique *Lemniscomys striatus* (Mammalia, Muridae).—Mammalia 44:73–82.
- Voss, R. S., & L. F. Marcus. 1992. Morphological evolution in muroid rodents II. Craniometric factor divergence in seven Neotropical genera, with experimental results from *Zygodontomys*.—Evolution 46:1918–1934.
- Wilson, D. E., & D. M. Reeder (eds.). 1993. Mammal species of the World, a taxonomic and geographic reference, Second Edition. Smithsonian Institution Press, Washington D. C., 1206 pp.
- Wroughton, R. C. 1906. On some mammals collected by Mr. Robin Kemp in S. Nigeria.—Annals and Magazine of Natural History, London, series 7, 17:375–379.
- Yalden, D. W., M. J. Largen, D. Kock, & J. C. Hillman. 1996. Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation.—Tropical Zoology 9:73–164.

Appendix 1.—Geographic coordinates of principal collecting localities mapped in Figure 12. Coordinates are presented either as extracted from the country gazetteers published by the United States Board on Geographic Names (= *G*) or as they appear on original specimen tags and in field catalogs, as designated by the collector (= *C*). To verify the equivalence of older placenames and currently recognized coordinates, we generally cross-referenced the cartographic information provided by Aggundey & Schlitter (1984), Davis & Misonne (1964), Delany (1975), Happold (1987), Rosevear (1965), Setzer (1956), and Swynnerton & Hayman (1951) with that contained in the USBGN gazetteers. Where directional and distance modifiers are given following a comma, the collector's coordinates apply specifically to that point from the named village or town.

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#### Algeria

Alger	36°47'N, 03°03'E <i>G</i>
Hammam Meskoutine	36°27'N, 07°16'E <i>G</i>
Hammam Rirha	36°23'N, 02°24'E <i>G</i>
Oran	35°42'N, 00°38'E <i>G</i>
Reghaia	36°44'N, 03°21'E <i>G</i>

#### Benin

Bimbereke	10°14'N, 02°40'E <i>C</i>
Diho	08°05'N, 02°31'E <i>C</i>
Guene	11°44'N, 03°13'E <i>C</i>
Kouande	10°20'N, 01°41'E <i>C</i>
Nikki	09°56'N, 03°13'E <i>C</i>
Porga	11°02'N, 00°58'E <i>C</i>
Segbana	10°56'N, 03°42'E <i>C</i>
Soubroukou	09°41'N, 01°38'E <i>C</i>
Zizonkame	07°55'N, 02°01'E <i>C</i>

#### Burkina Faso

Arly	11°34'N, 01°26'E <i>C</i>
Boussouma, 5 mi N	12°57'N, 01°05'W <i>C</i>
Cella, 1 km N	11°38'N, 00°22'W <i>C</i>
Cella, 6 mi S	11°32'N, 00°22'W <i>C</i>
Djipologo	10°56'N, 03°07'W <i>C</i>
Fo	11°53'N, 04°31'W <i>C</i>
Koutoura, 5 km SW	10°19'N, 04°53'W <i>C</i>
Nasso	11°13'N, 04°26'W <i>G</i>
Natiaboani	11°42'N, 00°30'E <i>C</i>
Nayoure, 3 km SE	12°15'N, 00°16'E <i>C</i>
Niangoloko	10°17'N, 04°55'W <i>G</i>
Nobere, 9 mi S	11°26'N, 01°10'W <i>C</i>
Orodara, 27 km	
ENE	11°04'N, 04°41'W <i>C</i>
Ougarou	12°10'N, 00°56'E <i>C</i>
Oulo	11°54'N, 02°58'W <i>C</i>
Seguenega, 6 mi SE	13°24'N, 01°55'W <i>C</i>

#### Cameroun

Boukma	08°32'N, 13°55'E <i>G</i>
Fort Foureau	12°05'N, 14°56'E <i>G</i>

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## Appendix 1.—Continued.

Garoua, 35 km S & 10 km E	09°06'N, 13°29'E C
Isiri	08°24'N, 14°36'E G
Kali	08°23'N, 14°21'E G
Koum	08°23'N, 14°31'E G
Maroua	10°35'N, 14°20'E G
Mora	11°03'N, 14°09'E G
Sir	10°36'N, 13°41'E G
Ghana	
Bangwon	10°58'N, 02°41'W C
Damango	09°04'N, 01°45'W C
Gambaga	10°31'N, 00°28'W C
Legon	05°40'N, 00°12'W C
Nabogo	09°45'N, 00°49'W C
Pirisi	10°07'N, 02°27'W C
Pulima	10°51'N, 02°03'W C
Sakpa	08°52'N, 02°21'W C
Shishe	10°42'N, 00°13'W C
Ivory Coast	
Bambela	09°37'N, 03°54'W G
Bouna	09°19'N, 02°53'W G
Kafiné	08°31'N, 05°19'W G
Kong	09°09'N, 04°37'W C
Ouangofetini	09°34'N, 04°03'W G
Tiebila (Tyébila)	09°45'N, 05°50'W G
Tyenko	08°14'N, 07°24'W C
Yama	09°36'N, 06°18'W C
Kenya	
Galma Galla	01°11'S, 40°47'E G
Kathekani	02°37'S, 38°09'E C
Kenya Karanzi	Not located
Kiboko	02°12'S, 37°42'E C
Kibwezi, 11 km N & 17 km E	02°19'S, 38°07'E C
Kilabasi	03°58'S, 38°57'E G
Lukenya Mountain	01°28'S, 37°03'E G
Machakos	01°31'S, 37°16'E G
Maktau (50 mi S)	03°24'S, 38°08'E G
Masi, Sand River	Not located
Maungu	03°33'S, 38°45'E G
Mtito Andei	02°41'S, 38°10'E G
Taveta	03°25'S, 37°42'E G
Voi	03°23'S, 38°34'E G
Mali	
Timbuktu (Timbocou)	16°49'N, 02°59'W G
Morocco	
Agadir, 15 km E	30°24'N, 09°28'W C
Aoulouz, 16 km W	30°42'N, 08°18'W C
Cap Spartel, 3 km S	35°46'N, 05°55'W C
Enzel (Anzel)	33°13'N, 05°58'W G
Essaouira, 5 km NE	31°31'N, 09°46'W C

## Appendix 1.—Continued.

Essaouira, 13 km E	31°30'N, 09°40'W C
Ifni	29°23'N, 10°10'W G
Marrakesh, 15 km WNW	31°53'N, 08°07'W ?
Meknès	33°54'N, 05°33'W G
Néfifik	33°43'N, 07°21'W G
Oued Cherrat	33°50'N, 07°07'W G
Oued Sebo	34°04'N, 04°56'W C
Oued Zem, 5 km S	32°49'N, 06°35'W C
Rabat, 15 km SW	33°57'N, 06°57'W C
Rabat, 17 km SW	33°55'N, 06°59'W C
Tamri, 8 km N	30°20'N, 09°50'W C
Taroudannt, 5 km S	30°26'N, 08°54'W C
Tiznit, 8 km S	29°38'N, 09°43'W C
Niger	
Farak	15°18'N, 08°55'E G
Gerari	13°46'N, 07°55'E G
Takoukout	15°07'N, 08°30'E G
Nigeria	
Bauchi	10°16'N, 09°50'E G
Borgu	09°52'N, 04°04'E G
Dada	11°34'N, 04°29'E C
Igbo Ora	07°26'N, 03°17'E G
Kabwir	09°24'N, 09°34'E G
Kishi	09°05'N, 03°51'E G
Mada River	08°54'N, 08°17'E C
Maiduguri, 22 mi S	11°33'N, 13°16'E C
New Bussa	09°53'N, 04°31'E G
Panyam	09°27'N, 09°09'E G
Panyam Fish Farm	09°27'N, 09°12'E C
Shagunu	10°21'N, 04°28'E C
Upper Ogun Ranch	08°09'N, 03°30'E C
Wawa	09°55'N, 04°27'E G
Yankari	09°45'N, 10°30'E G
Zaria	11°04'N, 07°42'E G
Senegal	
Bandia	14°37'N, 17°02'W G
Gemenjulla (Dié- oundialla)	13°13'N, 13°07'W G
Kotiari Naoudé	13°54'N, 13°27'W G
Koussanar	13°52'N, 14°05'W G
Sudan	
Agur	11°35'N, 30°28'E G
Badigeru Swamp	05°20'N, 32°02'E G
Bahr el Derof	Not located
Bahr al Ghazal	07°46'N, 27°40'E G
Delami (Dalami)	11°52'N, 30°28'E G
Duk Majak	09°05'N, 27°51'E G
El Fasher (Al Fa- shir)	13°38'N, 25°21'E G
Fashoda	09°53'N, 32°07'E G
Gallabat (Qallabat)	12°58'N, 36°09'E G
Gondokoro	04°54'N, 31°40'E G

## Appendix 1.—Continued.

Ikoto	04°06'N, 33°06'E <i>G</i>
Imurok	04°19'N, 32°24'E <i>G</i>
Juga Juga	13°48'N, 25°25'E <i>G</i>
Kadugli	11°00'N, 29°44'E <i>G</i>
Kaga Hills	13°50'N, 27°45'E <i>G</i>
Kudring	11°30'N, 30°06'E ?
Kuna	12°54'N, 32°31'E <i>G</i>
Li Rangu	04°43'N, 28°22'E <i>G</i>
Loa	03°48'N, 31°57'E <i>G</i>
Maridi	04°55'N, 29°28'E <i>G</i>
Molongori	04°10'N, 32°52'E <i>G</i>
Nimule	03°36'N, 32°03'E <i>G</i>
Nuba Mountains	10°40'N, 32°11'E <i>G</i>
Paloich	10°28'N, 32°32'E ?
Tadoro	10°41'N, 30°01'E <i>G</i>
Talodi (Talawdi)	10°38'N, 30°23'E <i>G</i>
Terrakekka (Terake- ka)	05°26'N, 31°45'E <i>G</i>
Torit	04°24'N, 32°34'E <i>G</i>
Torit, 30 km W	Not plotted
Juba-Torit, 80 km E	Not plotted
Umm Kaddadah	13°36'N, 26°42'E <i>G</i>
Tanzania	
Banagi	02°16'S, 34°51'E <i>G</i>
Dodoma, 50 mi N	Not located
Jumbe Kadala (Nda- la)	04°46'S, 33°16'E <i>G</i>
Manyara Lake	03°30'S, 35°50'E <i>G</i>
Mawere	Not located
Mdjengo's (Misinko)	04°45'S, 34°40'E <i>G</i>
Mtali's	04°22'S, 34°36'E <i>G</i>
Mwanza	02°31'S, 32°54'E <i>G</i>
Ndogowe	05°28'S, 34°22'E <i>G</i>
Pooma	04°59'S, 34°44'E <i>G</i>
Unyamwezi	04°–06°20'S, 32°–33°40'E <i>G</i>
Togo	
Dapango	10°52'N, 00°13'E <i>C</i>
Paio (Payo)	10°14'N, 00°41'E <i>C</i>
Pewa	09°17'N, 01°14'E <i>C</i>
Tunisia	
Algeriet	Not located
Cédria (Potinville)	36°42'N, 10°23'E <i>G</i>
La Marsa (Al Mar- sá)	36°53'N, 10°20'E <i>M</i>
Uganda	
Apeluk (Ajeluk)	01°30'N, 33°50'E <i>G</i>
Apoka	03°44'N, 33°43'E <i>C</i>
Kaiso Valley	01°31'N, 30°58'E <i>C</i>
Kananarock	03°58'N, 33°45'E <i>C</i>
Karamoja	03°43'N, 33°36'E <i>C</i>
Kidepo Valley Natl. Park	03°56'N, 33°42'E <i>G</i>
Loi Jome (Lotome)	02°24'N, 34°31'E <i>G</i>

## Appendix 1.—Continued.

Loirengiki	02°24'N, 33°54'E <i>G</i>
Lorupei	03°48'N, 33°40'E <i>C</i>
Malera	01°27'N, 34°03'E <i>G</i>
Nabilatuk	02°03'N, 34°35'E <i>G</i>
Nabumali	00°59'N, 34°13'E <i>G</i>
Rhino Camp	02°58'N, 31°24'E <i>G</i>
Tana River, near	00°08'N, 38°50'E <i>C</i>
Zaire	
Faradje	03°44'N, 29°43'E <i>G</i>
Niangara	03°42'N, 27°52'E <i>G</i>
Tingasi	03°24'N, 27°55'E <i>G</i>

Appendix 2.—Descriptive statistics for selected external and cranial variables and OTUs of the *Lemniscomys barbarus* group.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Total length				
<i>Lemniscomys barbarus</i>				
OTU 1	37	238.2	211–266	12.6
OTU 2	15	251.8	193–273	19.4
<i>Lemniscomys zebra</i>				
OTU 4	23	218.2	196–236	10.9
OTU 5	27	211.6	192–232	9.5
OTU 7	47	204.8	172–230	13.7
OTU 10	17	203.3	170–231	14.5
OTU 11	12	212.3	196–230	9.3
Tail length				
<i>Lemniscomys barbarus</i>				
OTU 1	37	127.0	110–145	10.5
OTU 2	14	139.7	130–148	6.0
<i>Lemniscomys zebra</i>				
OTU 4	23	120.4	105–134	8.0
OTU 5	27	114.7	105–130	6.8
OTU 7	47	112.2	91–130	8.7
OTU 10	17	112.1	98–162	14.5
OTU 11	12	113.9	109–120	2.7
Hindfoot length				
<i>Lemniscomys barbarus</i>				
OTU 1	44	27.1	24–29	1.0
OTU 2	15	28.7	27–30	0.9
<i>Lemniscomys zebra</i>				
OTU 4	25	25.2	24–27	1.0
OTU 5	32	25.3	23–27	1.0
OTU 7	51	25.5	23–27	0.9
OTU 10	21	24.4	23–25	0.7
OTU 11	12	24.3	22–27	1.6
Weight				
<i>Lemniscomys barbarus</i>				
OTU 1	44	45.8	28–56	5.9
OTU 2	15	55.5	38–69	8.9
<i>Lemniscomys zebra</i>				
OTU 4	23	26.3	18–31	3.4
OTU 5	32	25.9	18–34	4.2
OTU 7	51	25.6	20–34	3.5
Occipitonasal length				
<i>Lemniscomys barbarus</i>				
OTU 1	44	30.1	28.3–32.3	0.9
OTU 2	14	31.2	30.0–31.2	0.6
<i>Lemniscomys zebra</i>				
OTU 4	22	27.8	26.1–29.1	0.8
OTU 5	25	27.7	26.1–29.3	0.9

Appendix 2.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
OTU 7	51	27.2	25.9–29.1	0.8
OTU 10	12	27.1	25.7–28.6	1.1
OTU 11	12	27.9	26.4–29.1	0.8
Zygomatic breadth				
<i>Lemniscomys barbarus</i>				
OTU 1	43	14.2	13.6–15.1	0.4
OTU 2	14	14.7	13.7–15.7	0.5
<i>Lemniscomys zebra</i>				
OTU 4	22	12.7	11.9–13.4	0.4
OTU 5	25	12.7	11.8–13.9	0.4
OTU 7	51	13.0	12.2–13.8	0.4
OTU 10	12	12.6	11.7–13.3	0.5
OTU 11	12	13.3	12.6–14.1	0.5
Breadth of braincase				
<i>Lemniscomys barbarus</i>				
OTU 1	44	12.4	11.8–13.1	0.3
OTU 2	14	12.5	12.1–12.9	0.2
<i>Lemniscomys zebra</i>				
OTU 4	22	11.8	11.1–12.5	0.3
OTU 5	25	11.8	11.2–12.3	0.3
OTU 7	51	11.8	11.2–12.4	0.3
OTU 10	12	11.8	11.5–12.1	0.2
OTU 11	12	12.0	11.5–12.5	0.3
Interorbital breadth				
<i>Lemniscomys barbarus</i>				
OTU 1	44	4.7	4.4–5.1	0.2
OTU 2	14	4.9	4.5–5.3	0.2
<i>Lemniscomys zebra</i>				
OTU 4	22	4.5	4.0–4.9	0.2
OTU 5	25	4.5	4.1–4.8	0.2
OTU 7	51	4.3	4.0–4.8	0.2
OTU 10	12	4.3	4.1–4.6	0.2
OTU 11	12	4.3	3.9–4.5	0.2
Length of nasals				
<i>Lemniscomys barbarus</i>				
OTU 1	44	11.5	10.1–12.6	0.5
OTU 2	14	12.2	11.6–13.2	0.4
<i>Lemniscomys zebra</i>				
OTU 4	22	10.6	9.7–11.3	0.4
OTU 5	25	10.6	9.6–11.7	0.5
OTU 7	51	10.3	9.3–11.4	0.5
OTU 10	12	10.0	9.1–10.9	0.6
OTU 11	12	10.5	9.9–11.0	0.4
Postpalatal length				
<i>Lemniscomys barbarus</i>				
OTU 1	44	10.5	9.6–11.5	0.5
OTU 2	13	10.7	10.4–10.9	0.2



## Appendix 2.—Continued.

Species and OTU	<i>n</i>	Mean	Range	SD
<i>Lemniscomys zebra</i>				
OTU 4	22	9.4	8.5–10.3	0.4
OTU 5	23	9.4	8.8–10.3	0.4
OTU 7	51	9.1	7.6–10.0	0.4
OTU 10	12	9.3	8.5–10.1	0.6
OTU 11	12	9.8	9.3–10.7	0.5
Length of incisive foramen				
<i>Lemniscomys barbarus</i>				
OTU 1	44	5.9	5.4–6.6	0.2
OTU 2	14	6.2	5.7–6.5	0.2
<i>Lemniscomys zebra</i>				
OTU 4	22	5.4	4.7–6.0	0.3
OTU 5	25	5.5	4.9–5.9	0.3
OTU 7	51	5.2	4.5–5.9	0.3
OTU 10	12	5.2	4.5–5.6	0.3
OTU 11	12	5.4	5.0–5.8	0.3
Length of diastema				
<i>Lemniscomys barbarus</i>				
OTU 1	44	7.4	6.7–8.2	0.3
OTU 2	14	7.8	7.3–8.3	0.3
<i>Lemniscomys zebra</i>				
OTU 4	22	6.5	6.0–7.2	0.3
OTU 5	25	6.6	6.0–7.4	0.3
OTU 7	51	6.3	5.8–7.0	0.3
OTU 10	12	6.4	5.8–6.9	0.3
OTU 11	12	6.6	5.9–7.1	0.4
Palatal breadth across M1s				
<i>Lemniscomys barbarus</i>				
OTU 1	44	6.2	5.9–6.6	0.2
OTU 2	15	6.2	5.9–6.5	0.2
<i>Lemniscomys zebra</i>				
OTU 4	22	5.8	5.5–6.3	0.2
OTU 5	25	5.8	5.5–6.3	0.2
OTU 7	51	5.8	5.3–6.2	0.2
OTU 10	12	5.6	5.2–5.9	0.2
OTU 11	12	5.7	5.3–5.9	0.2
Breadth of zygomatic plate				
<i>Lemniscomys barbarus</i>				
OTU 1	44	3.8	3.4–4.3	0.2
OTU 2	14	3.9	3.4–4.3	0.2
<i>Lemniscomys zebra</i>				
OTU 4	22	3.4	3.0–3.9	0.2
OTU 5	25	3.4	3.1–3.8	0.2
OTU 7	51	3.4	3.0–3.8	0.2
OTU 10	12	3.3	3.1–3.7	0.2
OTU 11	12	3.5	3.3–3.8	0.1

## Appendix 2.—Continued.

Species and OTU	<i>n</i>	Mean	Range	SD
Alveolar length of maxillary toothrow				
<i>Lemniscomys barbarus</i>				
OTU 1	44	5.59	5.22–5.98	0.18
OTU 2	15	5.60	5.37–5.83	0.15
<i>Lemniscomys zebra</i>				
OTU 4	24	5.31	4.95–5.81	0.23
OTU 5	32	5.25	5.02–5.59	0.14
OTU 7	51	5.31	4.95–5.74	0.19
OTU 10	22	5.09	4.89–5.26	0.11
OTU 11	15	5.33	5.07–5.62	0.17
Width of first upper molar				
<i>Lemniscomys barbarus</i>				
OTU 1	44	1.73	1.61–1.86	0.06
OTU 2	15	1.74	1.68–1.83	0.05
<i>Lemniscomys zebra</i>				
OTU 4	25	1.66	1.54–1.82	0.07
OTU 5	32	1.68	1.57–1.82	0.07
OTU 7	51	1.71	1.54–1.84	0.07
OTU 10	22	1.61	1.48–1.73	0.06
OTU 11	15	1.68	1.56–1.80	0.05

OTU codes: 1, Morocco, Agadir Province; 2, Morocco, Khouribga and Rabat provinces; 4, northern Ivory Coast and western Burkina Faso; 5, Ghana and Togo; 7, Nigeria, Northern Region, Jos Plateau; 10, Sudan, Equatorial Province; 11, Kenya.